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New Tertiary pycnodonts from the Tilemsi valley, Republic of Mali

A. E. Longbottom

Geology series Vol 38 No 1 26 January 1984

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World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Geol.)

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The Geology Series is edited in the Museum's Department of Palaeontology
Keeper of Palaeontology: Dr H. W. Ball
Editor of the Bulletin: Dr M. K. Howarth
Assistant Editor: Mr D. L. F. Sealy

ISBN 0 565 07000 2
ISSN 0007–1471

British Museum (Natural History)
Cromwell Road
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Geology series
Vol 38 No 1 pp 1–26

Issued 26 January 1984

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New Tertiary pycnodonts from the Tilemsi valley, Republic of Mali

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Synopsis

Three new species of *Pycnodus, P. maliensis, P. zeaformis*, and *P. jonesae* are described from the Tertiary deposits of the Tilemsi valley, Republic of Mali. The presence of three other species *P. variabilis, P. munieri* and *P.* cf. *bowerbanki* is noted. The other Tertiary species of *Pycnodus* are redescribed and some synonymies are suggested. It is also suggested that tooth replacement occurs in *Pycnodus* species. Photographs of the holotypes of *Pycnodus pachyrhinus* and *Periodus koenigii* are here published for the first time.

Introduction

The rocks of the Tilemsi valley in northern Mali have long been of interest to geologists. The deposits in the valley range from the Maastrichtian to Middle Eocene. Above this lie terrestrial deposits of post-Eocene age. Several expeditions in the early part of this century recovered a few fossils and these were described by de Lapparent (1905). Furon (1955) described the geological history of north Africa (including the Sahara) but the most detailed work on the area was done by H. Radier who had spent many years studying the Gao region for the Direction des Mines de l'Afrique Occidentale Français. Radier (1959: 322) gives a detailed account of the work done up to 1959 and provides a very extensive bibliography:

Much has been written on the geology and invertebrate palaeontology of the area but there have been very few publications on the vertebrae fossils from the Tilemsi valley. Radier gives a faunal list for each horizon he describes but although he lists pycnodonts, *Ceratodus* sp., *Myliobatis* sp., *Pycnodus variabilis* Stromer, *Phosphichthys thomasi* Arambourg, *Eotrigonodon laevis* Priem, *Trichiurus plicidens* Arambourg, siluroids, *Rhinobatus*, dasyatids and trigonids, there has been very little description of the fish fossils from Mali. Goto (1981) has given a short description of a pycnodont dentition and Lavocat (1955) described dentitions of *Protopterus* sp. from Tamaguélelt.

In 1975 a French expedition to the Tilemsi valley collected many vertebrate fossils. In 1979/80 an Anglo-French expedition, and in 1981 a joint British Museum (Natural History) and Kingston Polytechnic expedition, visited the same area and collected many more vertebrate fossils from the Tertiary rocks, of which the majority were fishes. This paper describes the pycnodont dentitions collected during these three expeditions. Whilst comparing the Mali pycnodonts with other African and European species it became apparent that a revision of Tertiary *Pycnodus* species was needed and this is included in this paper.

The crushing teeth of *Pycnodus* are elliptical and smooth at least in the median rows. In this they differ from the other Tertiary pycnodont genera *Anomoeodus* (with very elongated curved median teeth), *Palaeobalistium* (with subcircular teeth), and *Coelodus* (having median teeth with an apical crenulated indentation). The pycnodont dentitions from Mali are all referred to the genus *Pycnodus* because of the tooth shape.

Bull. Br. Mus. nat. Hist. (Geol.) **38** (1): 1–26

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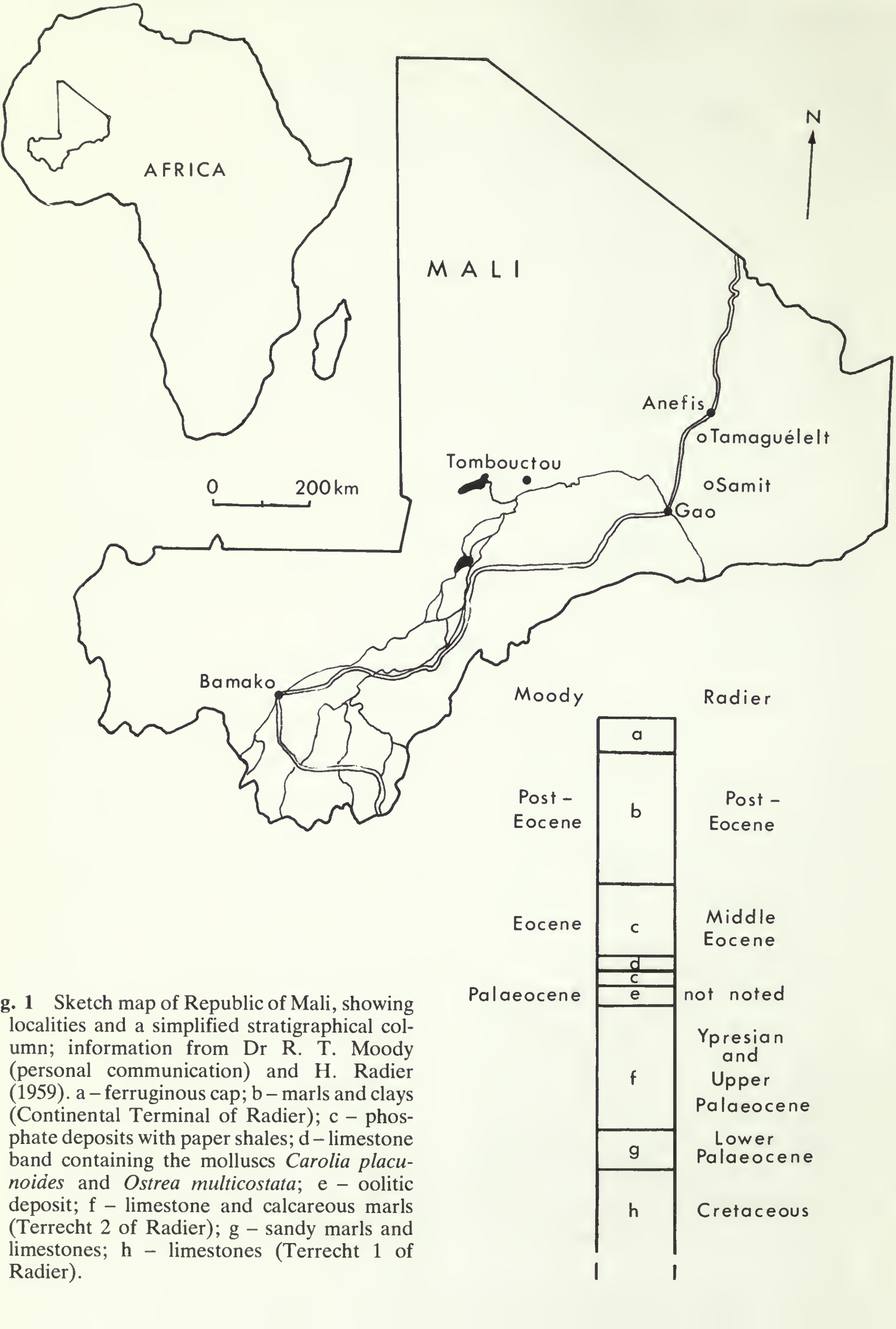
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c
Middle Eocene
d
c
Palaeocene
e
not noted
f
Ypresian and Upper Palaeocene
g
Lower Palaeocene
h
Cretaceous

Fig. 1 Sketch map of Republic of Mali, showing localities and a simplified stratigraphical column; information from Dr R. T. Moody (personal communication) and H. Radier (1959). a – ferruginous cap; b – marls and clays (Continental Terminal of Radier); c – phosphate deposits with paper shales; d – limestone band containing the molluscs *Carolia placunoides* and *Ostrea multicostata*; e – oolitic deposit; f – limestone and calcareous marls (Terrecht 2 of Radier); g – sandy marls and limestones; h – limestones (Terrecht 1 of Radier).

Sources of material and methods of study

The pycnodonts reported on here are represented by dentitions (splenials and vomers) only. The associated fish fauna includes many parts of catfish skeletons, *Brychaetus* sp., lungfish dentitions (including *Ceratodus humei* Priem), sparid and centropomid remains, *Myliobatis* sp. and rare sharks teeth. Other vertebrate (*Paleophis* sp., *Dyrosaurus* sp.) and invertebrate remains (molluscs) were also collected.

The pycnodont specimens were collected from two deposits. Most came from the phosphate deposits which have been dated by Radier (1959: 390) as Middle Eocene on the presence of the molluscs *Carolia placunoides* (Cantraine) and *Ostrea multicostata* Deshayes. The molluscs were collected from a limestone band occurring within the paper shales at the bottom of the phosphates. The vertebrate remains come from the phosphates themselves. Similar phosphate beds occur in many parts of north Africa but are usually considered to be at least as old as Ypresian elsewhere in Africa (R. T. Moody, personal communication).

A few pycnodont dentitions were collected from a coarse-grained deposit containing many very small ferruginous ooliths (0·75 mm in diameter). This deposit occurs underneath the lowest paper shale layer of the phosphate deposits. The fish fauna from the oolitic layer is similar to that of the phosphates except that, at the moment, *Ginglymostoma* cf. *angolense* Dartevelle & Casier, several unidentified teleosts, and the new *Pycnodus* cf. *bowerbanki* specimens are restricted to the oolitic deposit, whilst *Ceratodus humei* has only been found in the phosphates. The oolitic deposit was not recorded or described by Radier and no microfossils have yet been found to date it with precision. The deposit lies some way above the limestone from which Apostolescu (1961) described the ostracods *Uroleberis glabella* Apostolescu and *Ambocythere tatteuliensis* Apostolescu. These range throughout the Palaeocene. The oolitic deposit therefore cannot be older than Palaeocene or younger than Middle or Lower Eocene, depending on the age of the phosphate deposit. Madden *et al.* (1979) describe a deposit (the Umm Himar Formation) from the Harrat Hadan area of Saudi Arabia. Just below the fossiliferous horizon, but still in the Umm Himar Formation, in Saudi Arabia there is a deposit with small ferruginous ooliths and a root/burrow system very similar to that found in Mali. The fauna of the Umm Himar Formation is very similar to that from the oolitic deposit in Mali. Madden *et al.* (1979) date the Umm Himar Formation as Upper Palaeocene based on the first and last appearances of various elements in their fauna. They record *Ginglymostoma blanckenhorni* Stromer, *Ginglymostoma maghrebianum* Casier and catfish, all with a first appearance in the Palaeocene, and *Ceratodus humei* which has a last appearance in the Palaeocene (Tabaste 1963). In Mali *Ginglymostoma* cf. *angolense* (an Ypresian species) and catfish were found in the oolitic deposit. However, two specimens of *Ceratodus humei* were found in the overlying phosphates which contain molluscs thought to be Middle Eocene by Radier (1959: 378). This would be the youngest appearance of *Ceratodus humei* and casts doubt on the evidence of Madden *et al.* (1979) for a Palaeocene age of the Umm Himar Formation as based on the last appearance of *C. humei.*

The pycnodonts described herein were collected from two main localities, the first at Tamaguélelt about 25 km NNE of In Tasit, in the Gao region at 0° 15′ E, 17° 36′ N. Both the phosphates and the oolitic deposit occur around the Tamaguélelt outlier. The second site is about 30 km north-east of Samit wells at 1° 00′ E, 16° 50′ N, where only the oolitic deposit was explored. Fig. 1 shows the localities mentioned and a simplified stratigraphical column. The specimens are now in the collections of the British Museum (Natural History) (those numbered BMNH with or without a 'P' prefix) and in the Laboratoire de Paléontologie, Université de Pierre et Marie Curie, Paris (those with prefixes MLM and TGE). One specimen collected by Lavocat from an unknown locality in the Gao region is also included in the descriptions. This specimen is from the collections of the Laboratoire de Paléontologie de l'Université des Sciences et Techniques du Languedoc, Montpellier. Eighty-seven specimens were measured for the present study, of which 52 are splenials and 35 are vomers. The specimens are very well preserved and all those used in the following descriptions show more than one tooth row, and some of the specimens are almost complete. This is not usual in the study of Tertiary pycnodont

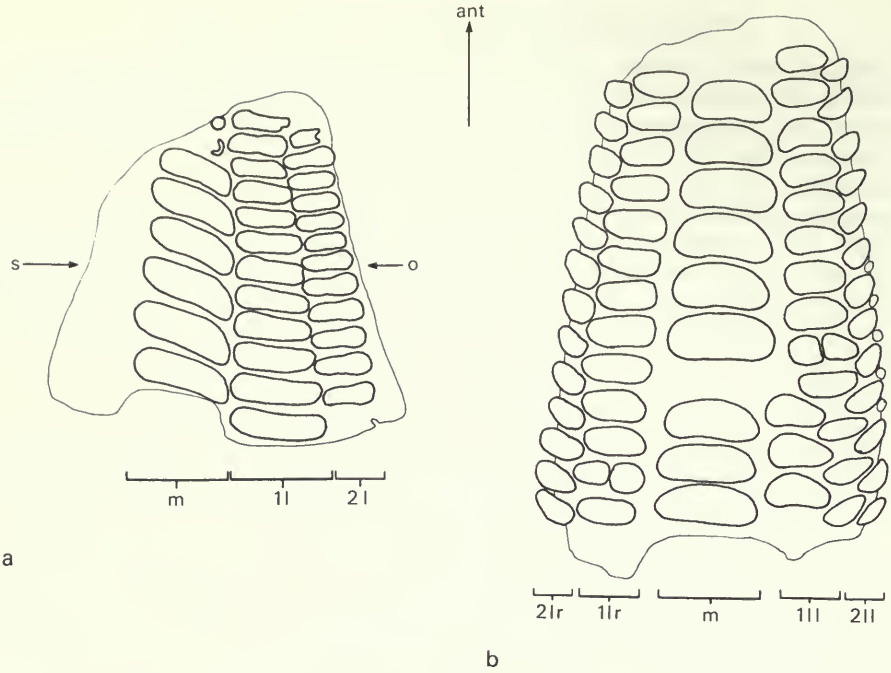


Fig. 2 Outline drawings of splenial and vomer to show terminology used; ant – anterior. a, splenial (lower dentition) of *P. maliensis* sp. nov.; m – medial row; 1l – first lateral row; 2l – second lateral row; s – symphyseal edge; o – outer edge. b, vomer (upper dentition) of *P. zeaformis* sp. nov.; m – median row; 1ll – first lateral row left; 2ll – second lateral row left; 1lr – first lateral row right; 2lr – second lateral row right. Directions refer to in-life position.

dentitions and allows very complete measurements and comparisons of the tooth rows on a large sample. It also allows some idea to be gained of the variation within a species. Most previous descriptions of species erected only on dentitions have been based on only one or two specimens, and those often very incomplete.

In the descriptions of the species in this paper the following terminology is used (Fig. 2). The tooth rows in the splenial are named medial for the innermost main row, first lateral for the next outer row, second lateral for the next outer and so on to the outermost row. Most of the specimens in the sample have only first and second lateral rows, but a few have more. In the vomer the tooth rows are named median for the row in the centre line, then first lateral (right and left) for the next outer rows on either side of the median row, then second lateral (right and left) and so on to the outermost rows. The individual teeth were measured such that length refers to the greatest anteroposterior measurement, and breadth (or width) refers to the greatest transverse measurement. The terms longer and shorter are relative to the first measurement, and the terms broader, wider and narrower are relative to the second. The length as a percentage of the breadth of each tooth has been measured and the average for each row calculated and used in the descriptions and tables as a character for comparing the species. Tooth shape in each row is another main character used to distinguish species.

Pycnodus dentitions usually have three main rows on the splenials and five on the vomers. However, this character is variable as is shown by the Mali specimens and extra rows may occur. In some cases this may be a growth phenomenon and what is normally a single row of elliptical teeth is instead represented by a double row of smaller teeth. Quite often in *Pycnodus* dentitions two small teeth occur where one would expect only one tooth in the main rows. It is also common to find that in the anterior region of the splenials and vomers the dental pavement is formed by many small and round, irregularly-arranged teeth. This indicates that *Pycnodus* dentitions can show quite a variation of tooth shape and it is only with great doubt that isolated pycnodont teeth can be identified. In the Mali fauna there are enough complete dentitions to see that, in general, three splenial and five vomerine tooth rows are present, whose teeth show fairly constant characters which can be used for identification purposes. In isolated specimens from other localities determinations can be positive only when at least three tooth rows are represented in one specimen.

The fauna from Mali contains two species based on splenials and four species based on vomers. Three of these species are new, the others being *P. variabilis* Stromer, *P. munieri* Priem, and *P.* cf. *bowerbanki* Egerton. It is likely that species erected only on splenials may be conspecific with those associated species erected on vomers, but in the Mali fauna there are no criteria for determining which if any of the splenial and vomerine species are conspecific since all the species occur at the one locality. Egerton (1877) suggested that upper and lower jaws tend to have similarly-shaped teeth and this would indicate that two of the new Mali species are the same, especially since they are of the same general size range. However, study of associated dentitions found in complete specimens in other pycnodonts does not seem to uphold this (R. Nursall, personal communication). The two species are therefore given different names.

Descriptions of new species

Infraclass **ACTINOPTERI** Cope, 1871
Series **NEOPTERYGII** Regan, 1923
Order **PYCNODONTIFORMES** Berg, 1940
Family **PYCNODONTIDAE** Agassiz, 1832
Genus ***PYCNODUS*** Agassiz, 1833

Pycnodus maliensis sp. nov.

Figs 2a, 3–8

DIAGNOSIS. Splenial dentitions with medial and first lateral teeth on average almost three times as wide as long; second lateral teeth on average slightly more than twice as wide as long; the outer ends of the medial teeth are turned posteriorly thus giving a bevelled appearance; medial teeth only 25% wider than the first lateral teeth.

NAME. After the country in which it is found.

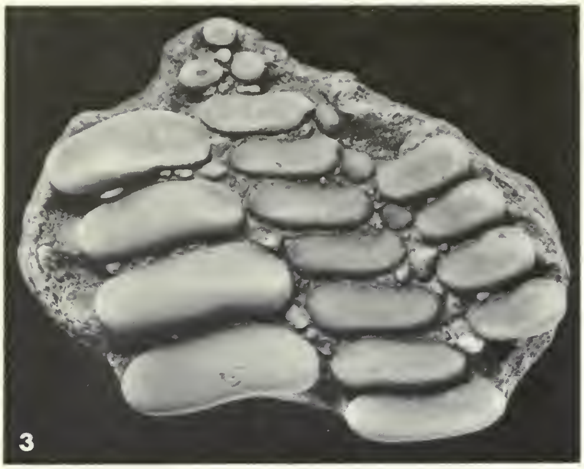
HOLOTYPE. BMNH P.61048, phosphate deposit, ? Middle Eocene. Tamaguélelt, Republic of Mali.

PARATYPES. TGE 601–18, MLM 1–15, BMNH P.60624–34, P.60919–20 (46 specimens).

OTHER MATERIAL. Fifty-six other specimens collected in 1981, and now in the collections of the British Museum (Natural History), are also identified as this species.

HORIZONS AND LOCALITIES. The holotype, paratypes and 49 of the other specimens were collected from the phosphate deposit at Tamaguélelt. Seven specimens were collected from the oolitic deposit at Tamaguélelt.

DESCRIPTION. The species is based on splenial dentitions only. The splenials are medium-sized compared with other *Pycnodus* species and the medial teeth of the type material average 12·8 mm in width. The medial teeth are more or less elliptical in shape but with a slightly convex anterior border and a slightly concave posterior border, especially towards the outer ends where the ends of the teeth turn posteriorly. The medial row usually has the largest teeth in which the width averages three times the length. The teeth in the first lateral row are also very wide compared to their length, the ratio being 3:1 again. The first lateral teeth are elliptical but the anterior border is slightly concave and the posterior one slightly convex. The teeth in the first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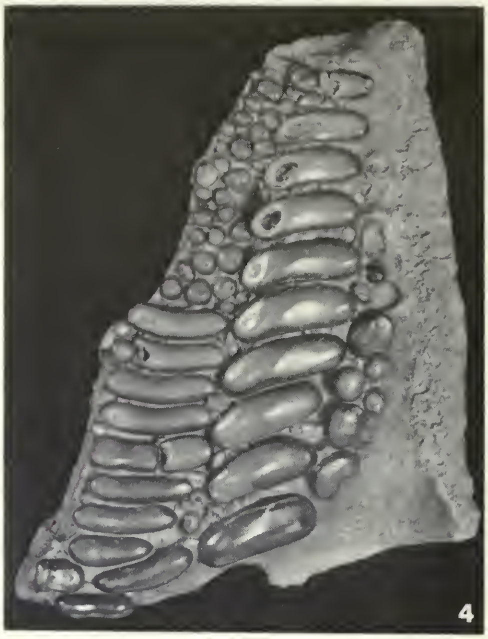
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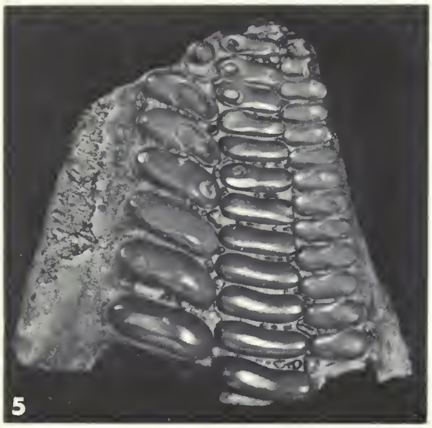
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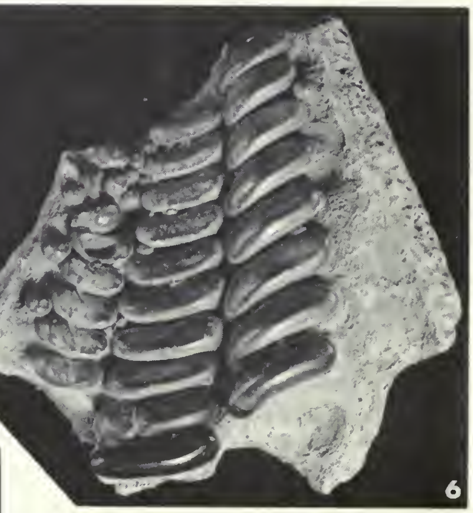
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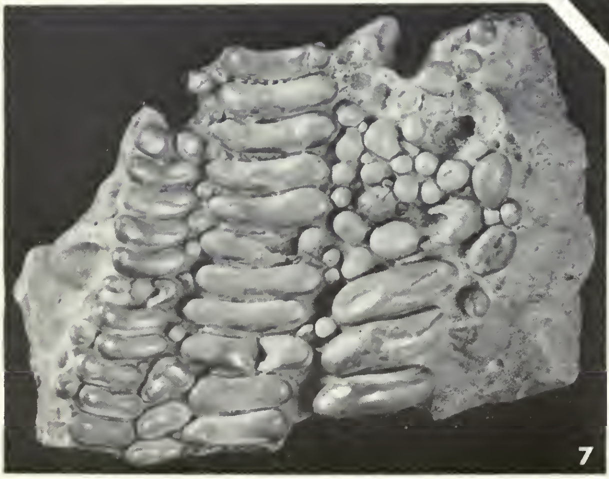
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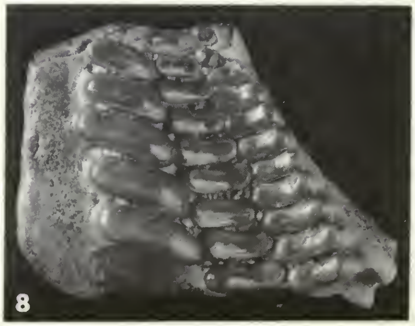
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Figs 3–8 Splenials of *P. maliensis* sp.nov., all except Fig. 3 ×1. Fig. 3, **holotype** BMNH P.61048, ×2. Fig. 4, paratype BMNH P.60631. Fig. 5, paratype BMNH P.60625. Fig. 6, paratype TGE 601. Fig. 7, paratype BMNH P.60628. Fig. 8, paratype BMNH P.60920.

lateral row are on average 9·9 mm wide. The teeth in the second lateral row are narrower, twice as wide as long and are also elliptical in shape with more or less parallel anterior and posterior borders. Small circular teeth commonly occur between the tooth rows and also in the anterior region of many of the splenials. The tooth-bearing surface of the splenial has a sinusoidal profile when viewed from behind. This is a character common to all *Pycnodus* species.

Pycnodus zeaformis sp. nov.

Figs 2b, 9–14

1981 'Pycnodont' Goto: ii–2; fig. 3; pl. 1.

DIAGNOSIS. Vomerine dentitions with median teeth on average 2·5 times as wide as long; first lateral teeth slightly more than twice as wide as long; second lateral teeth almost twice as wide as long; longest axes of teeth in lateral rows parallel to those of median teeth.

NAME. After the plant *Zea* because of the resemblance of the vomers to corn cobs.

HOLOTYPE. BMNH P.61049, phosphate deposit, ? Middle Eocene. Tamaguélelt, Republic of Mali.

PARATYPES. TGE 619–20, 622, 624, MLM 16–19, BMNH P.60640–3, P.60915, P.60921 (14 specimens).

OTHER MATERIAL. Eight other specimens collected in 1981, and now in the collections of the British Museum (Natural History), are also identified as this species.

HORIZONS AND LOCALITIES. The holotype, paratypes and seven other specimens were collected from the phosphate deposits at Tamaguélelt. One specimen was collected from the oolitic deposit at Tamaguélelt.

DESCRIPTION. The species is known by vomers only and these are medium-sized compared to those of other *Pycnodus* species. The width of the median teeth is 11 mm on average. The median row has the largest teeth and these are bean-shaped with a convex anterior border. The median teeth are about 2·5 times as wide as long. The first lateral teeth are subrectangular in shape and just over twice as wide as long, a feature not found in vomers of any other *Pycnodus* species. The first lateral teeth have their longest axes parallel to those of the median teeth. The teeth of the first lateral rows are shorter than those of the median row so that there are more lateral teeth per unit length. This means that some of the first lateral teeth are aligned with median teeth and some alternate with them. The teeth in the second lateral rows tend to alternate with those in the first lateral rows since they are about the same length. The second lateral teeth are ovoid or subrectangular and almost twice as wide as long. The longest axes in these are also parallel to those of the first lateral and median teeth, a character not present on the vomers of any other *Pycnodus* species. The teeth in the third and fourth lateral rows, where present, are ovoid and narrower than those of the second lateral rows. They have their longest axes parallel or at a slight angle to those of the other rows. The tooth-bearing surface of the vomer forms an arch when viewed from behind (Fig. 12), a character common in *Pycnodus* species.

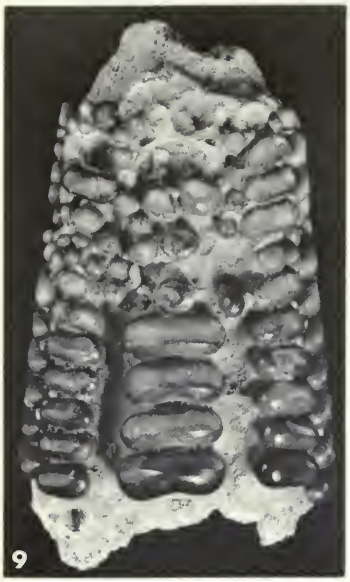
Pycnodus jonesae sp. nov.

Figs 15–17, 26b

DIAGNOSIS. Vomerine dentitions with elliptical or bean-shaped median teeth almost 2·5 times as wide as long; first lateral teeth just over 1·5 times as wide as long, with longest axes orientated at about 30° to those of median teeth; second lateral teeth only just wider than long and orientated at about 60° to median teeth.

NAME. In memory of Miss M. Jones who died on the 1979/80 expedition to Mali.

HOLOTYPE. BMNH P.61050, phosphate deposit, ? Middle Eocene. Tamaguélelt, Republic of Mali.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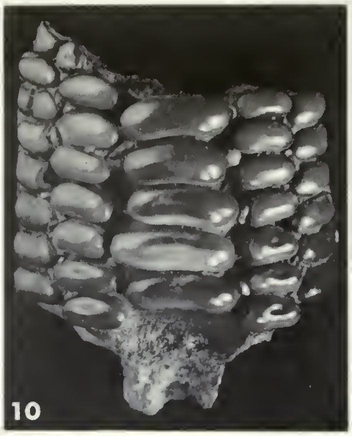
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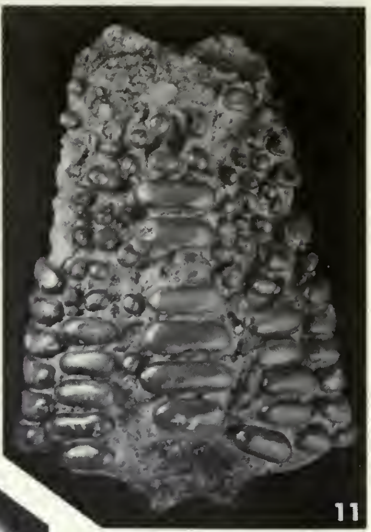
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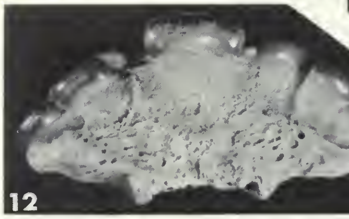
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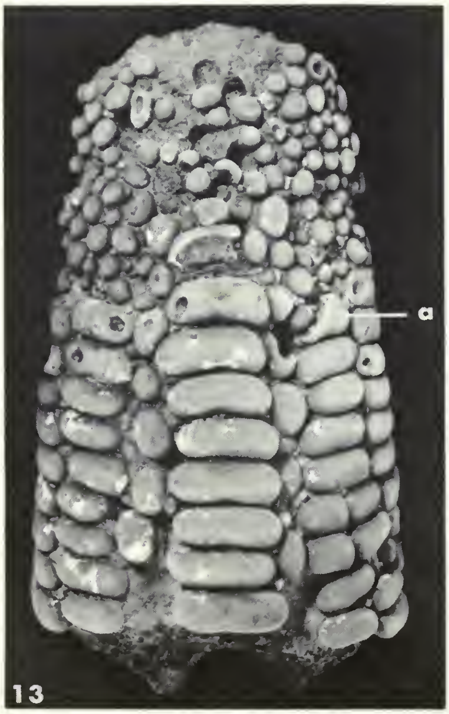

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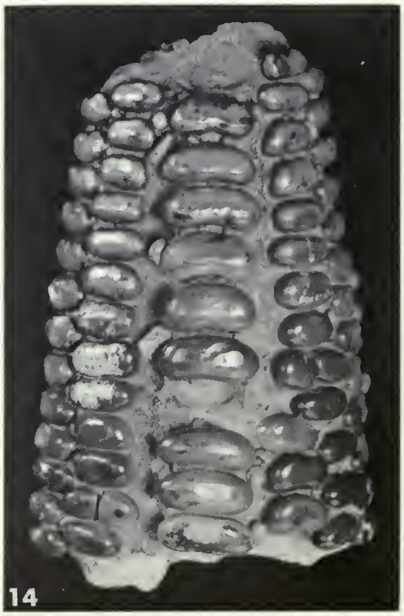
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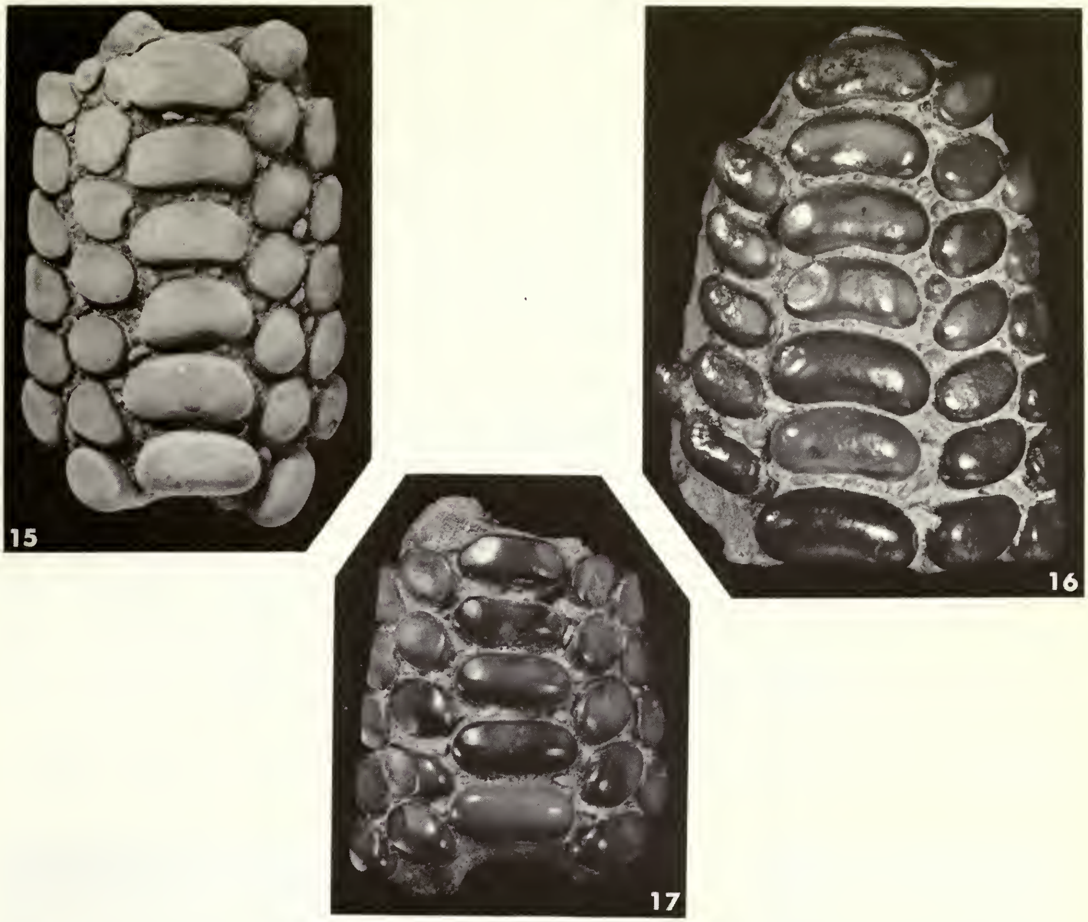
Figs 9–14 Vomers of *P. zeaformis* sp. nov., all ×1. Fig. 9, paratype TGE 620. Fig. 10, **holotype** BMNH P.61049. Fig. 11, paratype BMNH P.60921. Fig. 12, paratype BMNH P.60643, viewed from behind. Fig. 13, paratype BMNH P.60915 (*a* see text, p. 24). Fig. 14, paratype BMNH P.60643.



Figs 15–17 Vomers of *P. jonesae* sp. nov., all ×2. Fig. 15, paratype BMNH P.60636. Fig. 16, **holotype** BMNH P.61050. Fig. 17, paratype TGE 623.

Paratypes. TGE 623, MLM 20, 21, BMNH P.60636–7 (5 specimens).

Other material. Five other specimens collected in 1981, and now in the collections of the British Museum (Natural History), are also identified as this species.

Horizons and localities. The holotype, paratypes and four other specimens were collected from the phosphate deposit at Tamaguélelt. One specimen was collected from the oolitic deposit at Tamaguélelt.

Description. The species is known by vomerine dentitions only. These are on average slightly smaller than those of *Pycnodus zeaformis*, and have median teeth averaging 9·1 mm in width. The median teeth are elliptical or bean-shaped and almost 2·5 times as wide as long. This species differs from *P. zeaformis* in having oval first lateral teeth which have their longest axes orientated at about 30° to those of the median teeth. The first lateral teeth are just over 1·5 times as wide as long. The teeth of the second lateral rows are oval and marginally wider than long. Oval first and second lateral teeth are common in Tertiary *Pycnodus* species but *P. jonesae* differs from these in the shape of the median teeth and their greater relative width. The only other *Pycnodus* species with median teeth of the vomers 2·5 times as wide as long are *P. zeaformis*, which does not have oval lateral teeth, and *P. savini* Priem, which is much larger and has different-shaped median teeth (Fig. 26a). The tooth-bearing surface of *P. jonesae* forms an arch when viewed from behind.

Revision of the Tertiary species of *Pycnodus*

As stated in the Introduction many Tertiary species of *Pycnodus* have been erected on the basis of isolated vomerine and splenial dentitions, of varying completeness. Study of the great number of Mali pycnodont specimens, showing large parts of the dentition, has enabled me to appreciate the range of variability to be expected within any one species. On examining the figures and, in some cases, the material of other Tertiary species of *Pycnodus* I believe that some of them may simply be variants of one another. I will therefore suggest some synonymy. In a few

Table 1 Relative measurements[1] of the teeth of splenials of Tertiary *Pycnodus* species. (A) Length as a percentage of width of teeth, average of each tooth row with ranges given in brackets and number of specimens measured. (B) Average width of teeth in mm, all teeth in each row measured. (C) Average width of first lateral teeth as a percentage of average width of medial teeth.

	A				B		
	medial	first lateral	second lateral	number of specimens measured	medial	first lateral	C
P. maliensis	37·2 (29–46)	35·4 (25–47)	48·1 (33–61)	47	12·8	9·9	77·2
P. praecursor Cappetta's specimen	43·8	42·2	57·5	1	14	9·0	64·2
P. toliapicus + *P. koenigi*	46·6 (40–52)	68·9 (63–76)	80·3 (75–87)	6	15·0	8·6	57·3
Stromer's specimens of *P. variabilis* excluding St2	49·9 (45–58)	58·8 (53–70)	78·1 (65–100)	6	14	9·3	66
P. variabilis var. *togoensis*	51·1 (46–56)	56·0 (54–58)	77·9 (70–86)	3	11	7·4	67·2
P. praecursor D & C specimen	49·1	52·7	69·6	1	9·1	6·8	74·7
P. vasseuri	55·1	55·4	75	1	12	7·7	64·1
P. pellei	43·1	61·9	56·0	1	22	10·5	47·7
P. mokattamensis	56·2	80·5	53·8	2	20	11	55
Specimen St2	44·2	46·6	75·5	1	8	6·5	81·2
BMNH P.18823	42·6	42·3	—	1	7·2	5·3	73·6
P. bowerbanki	40·4	47·1	72·4	1	25·5	16·3	63·9
GAO 7	38·1	47·2	74·2	1	21·4	13·0	60·7
BMNH P.60917	48·2	45·3	75·3	1	21·7	13·1	60·3
Madden's large *Pycnodus* sp.	37·8	50	—	3 teeth only	31·6	—	—

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[1] A copy of the full measurements of the type material of *P. maliensis* is deposited in the Palaeontology Library of the British Museum (Natural History).

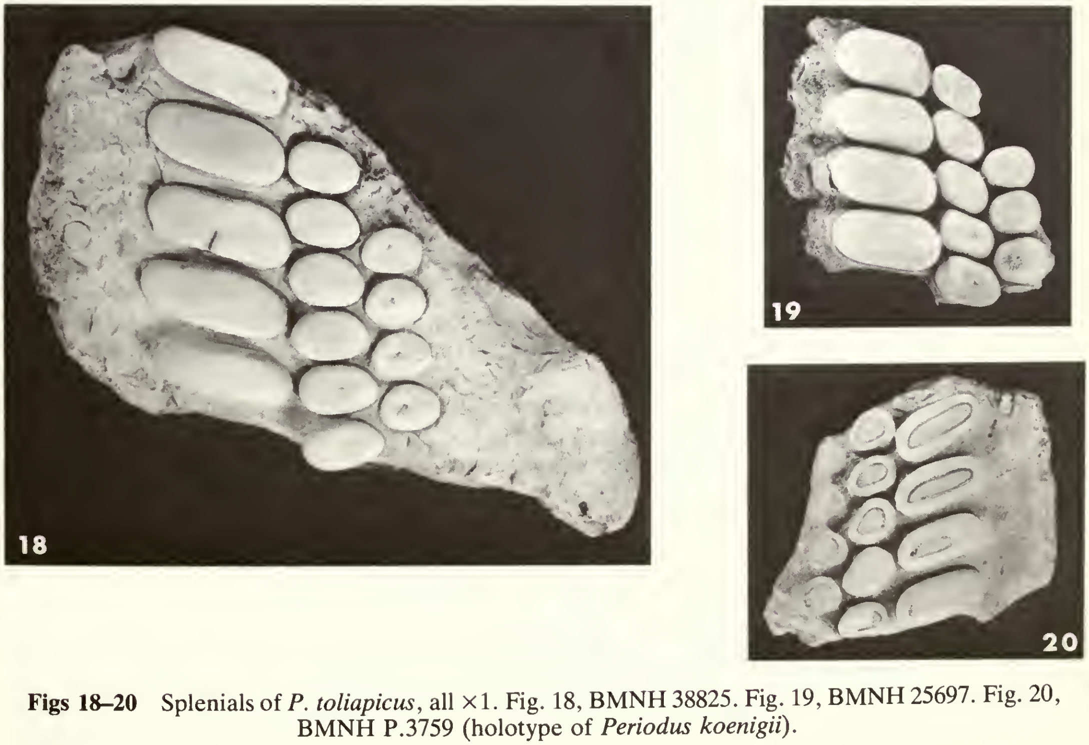
instances vomerine and splenial dentitions have been assigned to the same species, usually because they have been found in the same deposits. However, as we can only be certain of association of vomers and splenials in intact heads of pycnodonts I will treat splenial and vomerine material separately.

Splenials.
Table 1 is a comparison of the length as a percentage of the breadth of splenial teeth in Tertiary *Pycnodus* species.

Pycnodus toliapicus Agassiz
Figs 18–20

1839–44 *Pycnodus toliapicus* Agassiz: 196; pl. 72a, fig. 55. Ypresian, England.
1839–44 *Periodus koenigii* Agassiz: 201; pl. 72a, figs 61, 62 (misprinted in caption as figs 60, 61). Ypresian, England.
1850 *Periodus koenigii* Agassiz; Dixon: 205; pl. 10, fig. 13. Bracklesham beds, England.
1877 *Pycnodus toliapicus* Agassiz; Egerton: 53. Ypresian, England.
1895 *Pycnodus toliapicus* Agassiz; Woodward: 277. Ypresian, England.
1895 *Pycnodus koenigi* (Agassiz) Woodward: 278. Bracklesham beds, England; Middle Eocene, Belgium.
1905 *Pycnodus variabilis* Stromer: 101; pl. 16, figs 35, 37, *not* fig. 36. Middle Eocene, Egypt.
1910 *Pycnodus variabilis* var. *togoensis* Stromer: 485; figs 14a, b; textfig. 2. Landenian, Togo.
1920 *Pycnodus toliapicus* Agassiz; Bell: 12; pl. 11, fig. 16.
1935 *Pycnodus variabilis* var. *togoensis* Stromer; White: 40; fig. 9, *not* fig. 8. Landenian, Nigeria.
1950 *Pycnodus toliapicus* Agassiz; Casier: 23; pl. 2, fig. 6. Lutetian, Belgium.
1966 *Pycnodus toliapicus* Agassiz; Casier: 104; pl. 11, figs 4a–b. Ypresian, England.

The holotype of *Pycnodus toliapicus* is an incomplete specimen. At the same time Agassiz described *Periodus koenigii* based on a single worn splenial (BMNH P.3759). In 1877, whilst



Figs 18–20 Splenials of *P. toliapicus*, all ×1. Fig. 18, BMNH 38825. Fig. 19, BMNH 25697. Fig. 20, BMNH P.3759 (holotype of *Periodus koenigii*).

describing more specimens (BMNH 38825–6, Fig. 18) of *P. toliapicus*, Egerton suggested that *P. toliapicus* and *P. koenigi* were synonymous. After restudy of the holotypes and other specimens I agree with this suggestion. Woodward (1895: 278), in describing the two species, also says that they are usually considered to be synonymous. He erroneously cites the holotype of *P. koenigi* as BMNH 25697 (Fig. 19) from the Bracklesham beds, Sussex, Dixon collection. The specimen of *P. koenigi* figured by Agassiz is in fact BMNH P.3759 (Fig. 20) from the London Clay, Sheppey, Kent, from the Enniskillen collection. Woodward describes P.3759 as 'a small abraded specimen' of *P. toliapicus*, thus showing that he could not easily distinguish between *toliapicus* and *koenigi*. BMNH 25697 is the specimen figured by Dixon (1850), although Woodward does not mention this. Splenials of *P. toliapicus* differ from those of *P. maliensis* in all characters mentioned in the diagnosis (p. 5).

At this point I will discuss specimens referred to two named taxa, *Pycnodus variabilis* Stromer and *Pycnodus variabilis* var. *togoensis* Stromer (Figs 21a, c, d, h, i). Stromer (1905: 101) erected *P. variabilis* for specimens from the lowest Middle Eocene of Mokattam, Egypt. Stromer's splenials St5 and M1 (1905: pl. 16, figs 35, 37, St5 redrawn here as Fig. 21a) do not appear to differ significantly from the holotypes of *toliapicus* or *koenigi*. In fact Stromer recognized the similarity and stated that the specimen described by Dixon (1850) as *P. koenigi* is the same as his specimens and should be synonymized with them. Stromer, however, believed that his specimens and Dixon's specimen were different from *toliapicus* and *koenigi*. As stated above neither Woodward nor I regard Dixon's specimen as representing a species different from *koenigi* (Woodward even thought it was the holotype), or from *toliapicus*, and therefore the splenials St5 and M1 figured by Stromer should be assigned to the species *toliapicus*.

Another of Stromer's splenial specimens (St2; Stromer 1905: pl. 16, fig. 36, redrawn here as Fig. 21h) differs from the splenials St5 and M1 in that the medial and first lateral teeth are relatively wider in St2. The tooth proportions are also smaller (average width of medial teeth 8 mm) than the other splenials (average width of medial teeth 14 mm) figured by Stromer. Stromer noted the differences in his specimens (hence the name *variabilis*) but did not think they warranted different species. I, however, believe that the differences are significant enough for St2 to be regarded as a different species from the other splenials, since in the proportions of the medial and first lateral teeth St2 differs from the other *variabilis* splenials as much as Stromer's specimens St5 and M1 differ from *P. maliensis* splenials. St2 resembles *P. maliensis* in the proportions of the medial and first lateral teeth (which fall just within the upper limit of *maliensis*). However, the second lateral teeth are subcircular in St2 and very different from those in *maliensis*. Because of the relatively wide medial and first lateral teeth St2 differs from other Tertiary *Pycnodus* species, and therefore remains identified as *P. variabilis* (p. 17). The other splenials described by Stromer (1905: 191) as *P. variabilis* but not figured appear, from the measurements and descriptions given, to be similar to St5 and M1, but without examination of the specimens I cannot be definite about their identification.

Stromer (1910: 485; figs 14a, b, fig. 2) described *Pycnodus variabilis* var. *togoensis* on splenials, from the Landenian (Leriche 1913) of Adabion, Togo. White (1935: 40; fig. 9) refers a similar specimen from the Landenian of Sokoto, Nigeria to this variety also. I can see no difference between this variety and Stromer's St5 and M1. The medial teeth are supposed to be relatively wider in var. *togoensis*, but the difference is very slight except in the much larger specimen shown by Stromer (1910: fig. 2) which is in fact very similar to Egerton's specimens of *P. toliapicus*, BMNH 38825–6 (Fig. 18). The specimen figured by White (1935: fig. 9, BMNH P.18824, redrawn as Fig. 21c) has medial teeth of the same proportions as those of St5 and M1. White's reason for identifying his specimens as *P. variabilis* var. *togoensis* rather than *P. variabilis* was their association with large individual teeth of similar proportions to the large specimen figured by Stromer (1910: fig. 2) as *P. variabilis* var. *togoensis*. Because of their similarity to St5 and M1 the specimens identified by Stromer as *P. variabilis* var. *togoensis* and BMNH P.18824 should be assigned to *P. toliapicus*.

BMNH P.18823, a splenial from the Landenian of Gada, Nigeria, described by White (1935: 40; fig. 8, redrawn here as Fig. 21i) as *P. variabilis* var. *togoensis* differs from both BMNH P.18824 and Stromer's examples of *P. variabilis* var. *togoensis* in having relatively wider medial

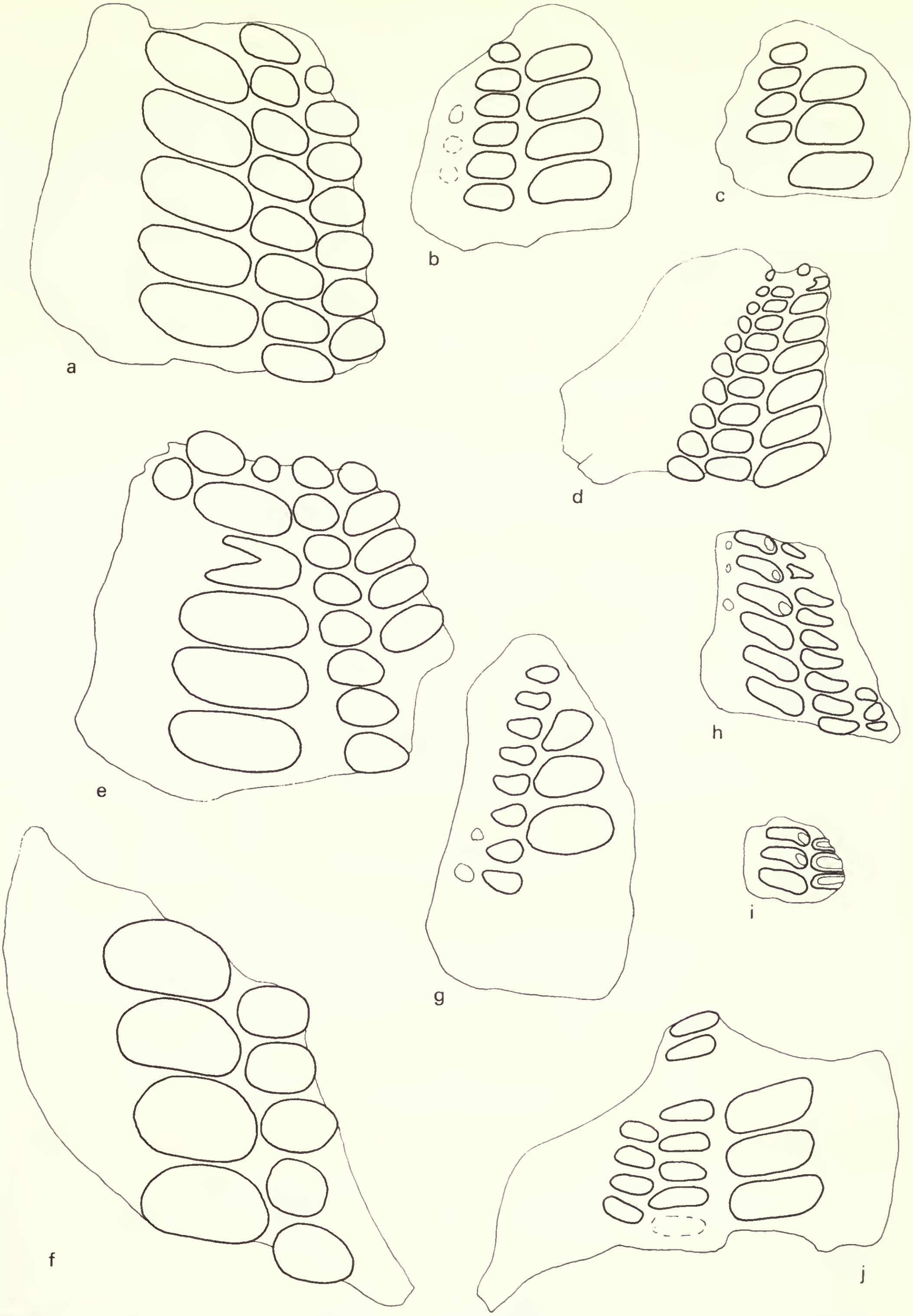


Fig. 21 Outline drawings of splenials of *Pycnodus* species to show differences in tooth shapes. All ×1, drawn from original photographs or drawings. a, *P. variabilis*, St5. b, *P. praecursor*. c, *P. variabilis* var. *togoensis*, BMNH P.18824. d, *P. variabilis* var. *togoensis*. e, *P. pellei*, holotype. f, *P. mokattamensis*. g, *P. vasseuri*, holotype. h, *P. variabilis*, St2. i, *P. variabilis* var. *togoensis*, BMNH P.18823. j, *P.* cf. *praecursor*.

and first lateral teeth. In these respects it resembles Stromer's (1905) St2, as White himself points out (1935: 42). Like St2 the proportions of the medial and first lateral teeth of BMNH P.18823 fall within the range of those of *P. maliensis*, but because of the lack of second lateral teeth it is not possible to say whether P.18823 is an example of *P. maliensis* or the same as St2. The teeth of BMNH P.18823 and St2 are similar in size and smaller than most specimens of *P. maliensis*; it is therefore probable that BMNH P.18823 is the same species as St2, that is *P. variabilis* as restricted here.

Pycnodus praecursor Dartevelle & Casier
Fig. 21b

1943 *Pycnodus variabilis* Stromer; Dartevelle & Casier: 90, name only.
1949 *Pycnodus praecursor* Dartevelle & Casier: 212; pl. 17, figs 1, 3 (?4, 5). Palaeocene (Montian), Landana, Angola.

This species differs from *P. maliensis* in all characters listed on p. 5. It is not significantly different from *P. toliapicus*. Dartevelle & Casier suggested that *praecursor* is similar to *variabilis* (as defined by Stromer) but ancestral to it because of its earlier occurrence. The splenials of *praecursor* are similar to Stromer's St5 and M1 and I believe that they should be reassigned to *P. toliapicus* also.

Cappetta (1972: 222; pl. 11, figs 3, 4) described two splenials from the Palaeocene of Niger as *Pycnodus* cf. *praecursor*. However, one specimen (1972: pl. 11, fig. 3, redrawn here as Fig. 21j) differs from those described by Dartevelle & Casier in having relatively wider medial, first lateral and second lateral teeth. The proportions of these teeth fall within the range of those of *P. maliensis*, but this specimen does not have the bevelled medial teeth characteristic of *maliensis*. The other specimen figured by Cappetta (pl. 11, fig. 4) has medial teeth only but the proportions of these fall within the range of those of *maliensis*. Without the first and second lateral teeth it is not possible to confirm whether this specimen is *maliensis* or, for example, *P. pellei* which also has medial teeth of similar proportions.

Pycnodus vasseuri Savornin
Fig. 21g

1915 *Pycnodus vasseuri* Savornin: 376; fig. 5. Ypresian, Tocqueville, Algeria.

The species is based on one splenial. The photograph in Savornin's paper is very indistinct but measurements given by Savornin show that this specimen differs in tooth proportions from *P. maliensis*. It appears to be similar to *P. toliapicus* and probably should be synonymized with it.

Pycnodus pellei Priem
Fig. 21e

1903 *Pycnodus pellei* Priem: 402; pl. 13, fig. 5. Lower Eocene, Gafsa, Tunisia.
1952 *Pycnodus pellei* Priem; Arambourg: 229; pl. 37, fig. 29. Lower Eocene, Kouif, Algeria.

This species is known only by two splenial dentitions. The average length/breadth index of the medial teeth of *P. pellei* falls just within the upper limit of that of *P. maliensis*. However, the first and second lateral teeth of *pellei* are so much narrower than those of *maliensis* that they are obviously distinct species. The splenials of *P. pellei* resemble Stromer's specimens St5 and M1 but as Stromer says the first lateral teeth are slightly narrower in *pellei*, the medial and second lateral teeth slightly wider and the teeth of *P. pellei* are larger (average width of medial teeth 22 mm) than St5 and M1. Considering the small number of specimens involved I cannot say whether these differences are significant enough to warrant separation of *P. pellei* splenials and St5 and M1 into different species.

Pycnodus mokattamensis Priem
Fig. 21f

1897 *Pycnodus mokattamensis* Priem: 217; pl. 7, fig. 11. Lowest Lutetian, Mokattam, Egypt.
1899 *Pycnodus mokattamensis* Priem; Priem: 241; pl. 2, fig. 1. Lowest Lutetian, Mokattam, Egypt.

Two incomplete splenials of this species have been described. The splenials differ from those of *P. maliensis* in all of the characters listed in the diagnosis (p. 5). The splenials also differ from *P. toliapicus* (and synonyms) and *P. pellei* in having relatively narrow medial teeth which are oval in shape. *P. mokattamensis* also has narrower subcircular first lateral teeth.

Pycnodus bowerbanki Egerton
Figs 22–24

1877 *Pycnodus bowerbanki* Egerton: 4; pl. 3, fig. 2. Ypresian, England.
1895 *Pycnodus bowerbanki* Egerton; Woodward: 279.
1966 *Pycnodus bowerbanki* Egerton; Casier: 106; pl. 11, fig. 6.

This is the largest (average width of medial teeth 25·5 mm) of the Tertiary *Pycnodus* species and was previously known by one splenial only (BMNH 38824, Fig. 23). It is similar to *P. toliapicus* except that the medial and first lateral teeth of BMNH 38824 are relatively wider. It resembles *P. maliensis* in the proportions of the medial and first lateral teeth. However, the second lateral teeth are subcircular and only just wider than long. Because of this and the overall larger size *bowerbanki* is considered a separate species.

The specimen labelled GAO 7 (Fig. 24) collected by Lavocat from Mali, two almost complete splenials BMNH P.60916–7 (Fig. 22) and several fragments showing one or two tooth rows collected during the 1981 expedition differ significantly from the other Mali splenials. These specimens have larger teeth (average width of medial teeth 21·7 mm) than *P. maliensis* specimens and the medial teeth are not bevelled at the outer end. The first laterals are rectangular and twice as wide as long. The major difference from *maliensis* is that the present specimens have subcircular rather than elliptical second lateral teeth. The tooth proportions of these specimens are extremely similar to those of *P. bowerbanki* and they are therefore identified as *P.* cf. *bowerbanki*. All of these larger specimens collected on the 1981 expedition come from the oolitic deposit. Most were collected at Tamaguélelt but one specimen (BMNH P.60917) is from the oolitic deposit at the Samit locality.

Madden (1982) reports pycnodont teeth from the Umm Himar Formation, Saudi Arabia. He describes three medial teeth and one first lateral tooth from a large *Pycnodus* species. Madden's specimens are slightly larger than medial teeth of *bowerbanki* and represent the largest Tertiary *Pycnodus* known. The proportions of the medial teeth from Saudi Arabia are very similar to those of *bowerbanki*. No complete specimens have been found in the Umm Himar Formation and without second lateral teeth it is not possible to identify this large *Pycnodus* species. However, the Mali specimens show that large *Pycnodus* specimens, very similar to *bowerbanki*, do occur in Africa and it is possible that Madden's large *Pycnodus* sp. teeth are the same as the Mali ones and *P. bowerbanki*.

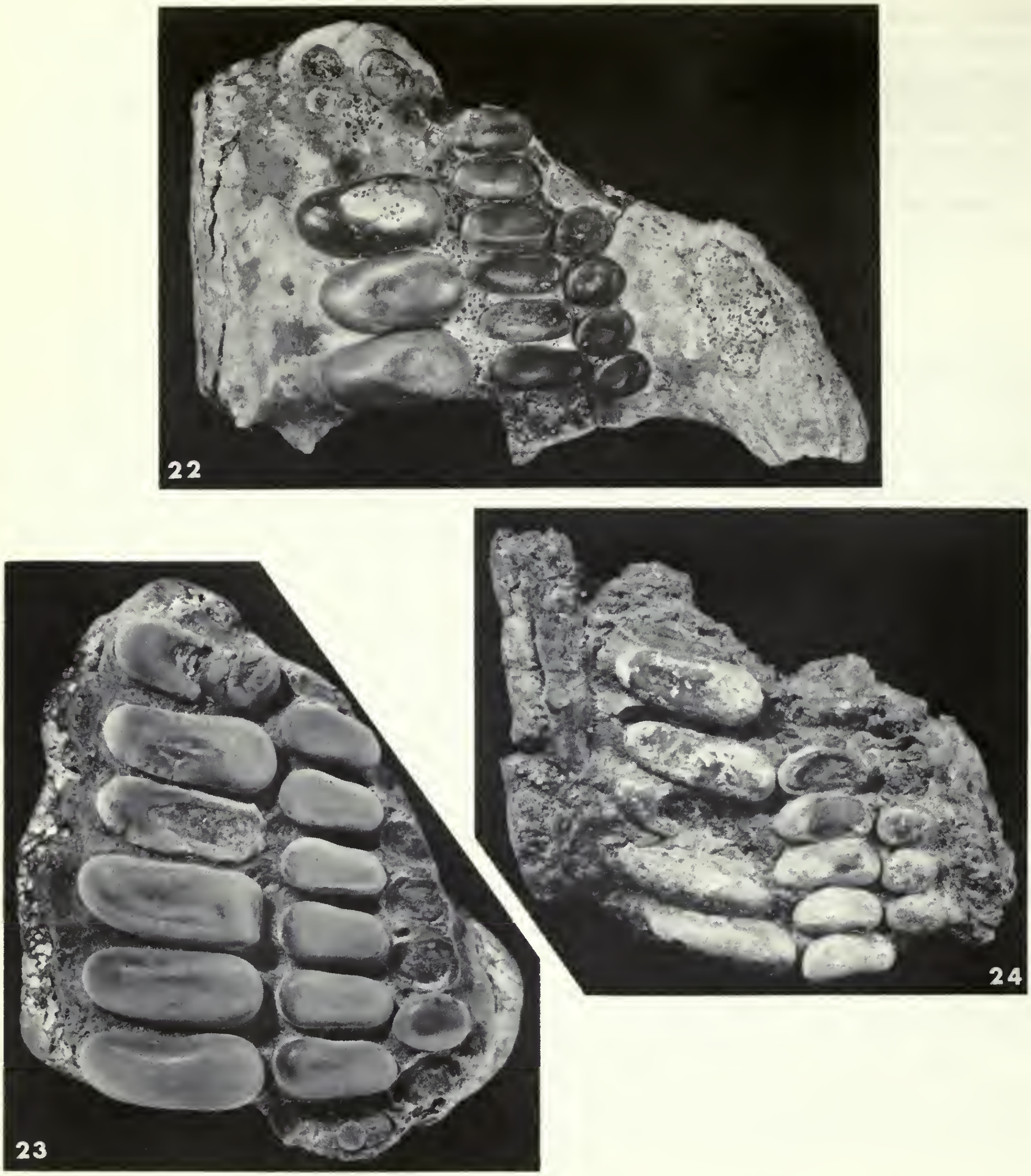
Vomers

The species where vomerine dentitions are known are reappraised and compared with each other and with *P. zeaformis* and *P. jonesae*. The length as a percentage of the breadth of vomerine teeth of Tertiary *Pycnodus* species is given in Table 2.

Pycnodus variabilis Stromer
Figs 25a–c, 27

1905 *Pycnodus variabilis* Stromer: 191; pl. 16, figs 33, 34. Lowest Middle Eocene, Mokattam, Egypt.

Stromer described two vomers under this name. They have narrow subtriangular median teeth with a very convex anterior border and a straight posterior border. The first lateral teeth are



Figs 22–24 Splenials of *P. bowerbanki*, all ×1. Fig. 22, BMNH P.60917. Fig. 23, holotype BMNH 38824. Fig. 24, GAO 7.

small and not much wider than long. They alternate with the median teeth and are shaped like an asymmetrical triangle with the greatest height nearer the midline of the vomer. In this respect they differ from other Tertiary species. The second lateral teeth are subtriangular to oval and have their longest axes at 60°–90° to those of the median teeth. The outer edges of the second lateral teeth are often worn and this accentuates their anteroposterior length. This is the shape and orientation of second lateral teeth found most in *Pycnodus* vomers. *P. variabilis* vomers therefore differ from *P. zeaformis* in all characters mentioned in the diagnosis (p. 7), and from

Table 2 Relative measurements[2] of teeth of vomers of Tertiary *Pycnodus* species. (A) Length as a percentage of width of teeth, average of each tooth row with ranges given in brackets and number of specimens measured. (B) Average width of teeth in mm, all teeth in each row measured.

	A				B	
	median	first lateral	second lateral	number of specimens measured	median	first lateral
P. zeaformis	40·7 (36–49)	45·8 (39–51)	52·9 (42–68)	15	11·0	7·5
P. jonesae	44·6 (39–52)	65·0 (56–78)	71·1 (64–86)	6	8·9	5·4
P. variabilis	70 (69–71)	88 (75–101)	163	2	5·6	4·1
P. praecursor	65·8	113	125	1	5·6	4·5
TGE 625	69·7	96·9	156	1	4·6	3·4
P. tattami	62·2	70·4	110	1	12·6	8·8
P. thamallulensis	60·6	85	—	1	15	10
P. mokattamensis	71·9	75	137	1	14	12
P. munieri	63·3	81·2	154	1	11	8
P.60635	55·9	72	157	1	6·7	4·5
P.10121	65	77	148	1	11·7	8·3
P. lemellefensis	54	66·6	100	1	18	12
P. legrandi	60·6	66·6	125	1	16	12
P. savini	51·1	75	122	1	22	12
P. pachyrhinus	62 (60–64)	73 (72–74)	138·5 (130–147)	2	11·8	8·8

[2] A copy of the full measurements of type material of *P. zeaformis* and *P. jonesae* is deposited in the Palaeontology Library of the British Museum (Natural History).

P. jonesae in the shape of the median teeth. The vomers were identified as *P. variabilis* by Stromer because of their association with splenials he described as *variabilis*. The vomers differ from previously described species in the shape of the median and first lateral teeth and so there is no reason to reassign the vomers, unlike the splenials where it is suggested (p. 12) that all but St2 (Stromer 1905: pl. 16, fig. 36) be reassigned.

In the Mali fauna the smallest vomer, TGE 625 (average width of median teeth 4·8 mm) (Figs 25c, 27), is very different from the others. It is identified as *P. variabilis* because it has narrow subtriangular median teeth, triangular first lateral teeth with their apices nearer the midline, and oval second lateral teeth orientated at 70°–90° to the median teeth.

Pycnodus praecursor Dartevelle & Casier

Fig. 25d

1949 *Pycnodus praecursor* Dartevelle & Casier: 212; pl. 17, figs 7a, b. Palaeocene, Landana, Cabinda, Angola.

The vomers figured by Dartevelle & Casier resemble the vomers of *P. variabilis*. They have triangular median and first lateral teeth and oval second lateral teeth. These vomers therefore

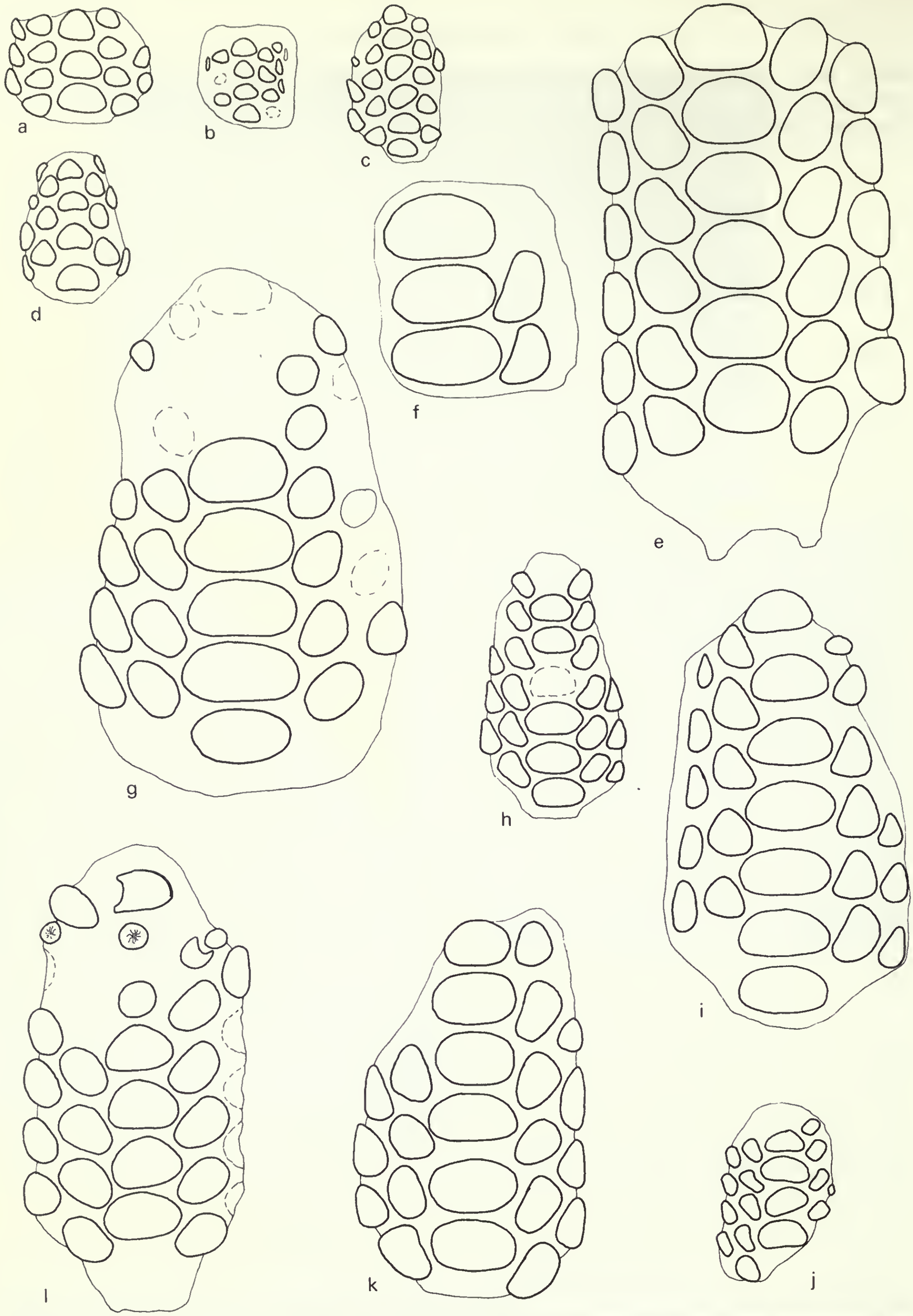


Fig. 25 Outline drawings of vomers of *Pycnodus* species to show differences in tooth shapes. All ×1, drawn from original photographs or drawings. The first and second lateral row teeth are slightly foreshortened. a, *P. variabilis*, specimen St. b, *P. variabilis*, specimen M. c, *P. variabilis*, TGE 625. d, *P. praecursor*. e, *P. mokattamensis*, holotype. f, *P. legrandi*, holotype. g, *P. lemellefensis*, holotype. h, *P. munieri*. i, *P. munieri*, holotype. j, *P. munieri*, BMNH P.60635. k, *P. toliapicus*, BMNH P.10121. l, *P. pachyrhinus*, holotype BMNH P.610.

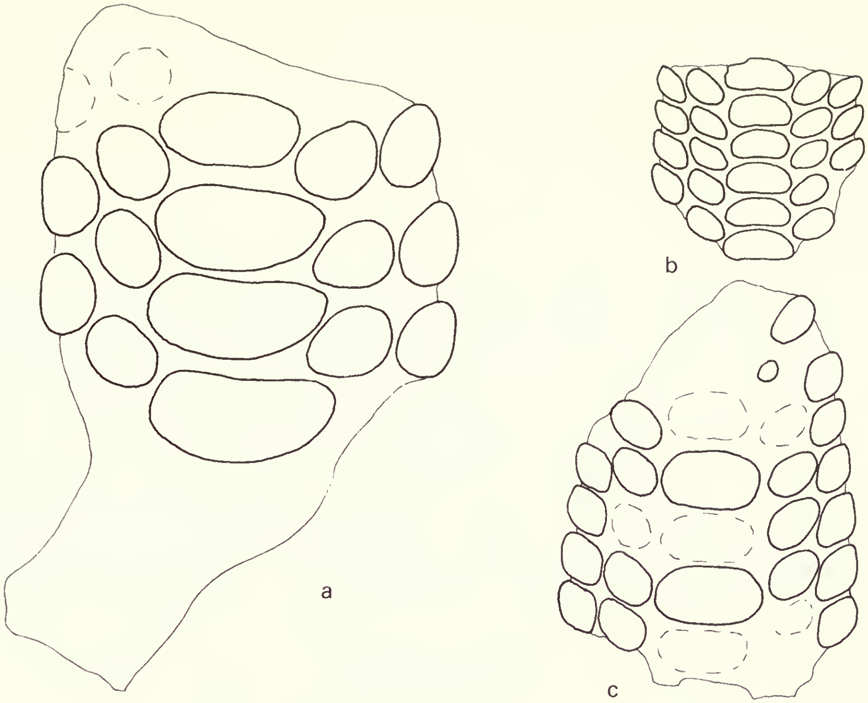


Fig. 26 Outline drawings of vomers of *Pycnodus* species, continued from Fig. 25. All ×1, drawn from original photographs or drawings. a, *P. savini*, holotype. b, *P. jonesae*, MLM 21. c, *P. tattami*, holotype BMNH P.18825.

differ from *P. zeaformis* and *P. jonesae*. Dartevelle & Casier say that the vomers resemble those of *P. tattami* in the width and open spacing of the median teeth. However, the median teeth of *P. tattami* are rectangular and the first lateral teeth are oval and not like those of *P. praecursor*. *P. praecursor* vomers should therefore be synonymized with *P. variabilis* vomers under the latter name.

Pycnodus tattami White
Fig. 26c

1935 *Pycnodus tattami* White: 42; figs 10,11. Landenian, Wurno, Nigeria.

The species is based on two specimens. The holotype (BMNH P.18825) is a medium-sized vomer (average width of median teeth 12 mm) differing from *P. zeaformis* in all characters mentioned in the diagnosis (p. 7). The proportions of the teeth in *P. tattami* are similar to those of *variabilis* but the tooth shape is different. The median teeth in *tattami* are rectangular and relatively slightly wider than those of *variabilis*. The first laterals are ovoid and are orientated at about 30° to the median teeth. The second lateral teeth differ from those of all other species in being square or lozenge-shaped with their longest axes at about 45° to those of the median teeth. The second specimen described by White (BMNH P.18826) is much smaller than the holotype and White suggested that it was a juvenile and that the differences between the two are due to growth. The similarities he used to unite the two are the proportions of the teeth and the alignment rather than alternation of the first lateral and median teeth. White thought this arrangement was not found in any other Eocene species. This character is found in *P. zeaformis* but both specimens of *P. tattami* differ from *P. zeaformis* in other respects. The smaller specimen of *P. tattami* does not seem to be assignable to any other Tertiary species, and I leave it as *P. tattami* despite the differences from the holotype.

Pycnodus mokattamensis Priem
Fig. 25e

1897 *Pycnodus mokattamensis* Priem: 217; pl. 7, figs 9, 10. Lower Lutetian, Mokattam, Egypt.
1915 *Pycnodus mokattamensis* Priem; Savornin: 371; fig. 1. Ypresian, Rilassa, Algeria.
1922 *Pycnodus mokattamensis* Priem; Leriche: 208; pl. 4, fig. 6. Lower Lutetian, Mokattam, Egypt.

Three vomers of *P. mokattamensis* have been described. All three resemble *P. variabilis* in having median teeth with arched anterior borders. However, the first lateral teeth of *mokattamensis* are oval to subtriangular and wider at the posterior end. Some of the first lateral teeth also have a slightly concave inner anterior border. The second lateral teeth are oval and have the longest axes at 90° to those of the median teeth. Most of the teeth have a central depression and crenulations around the edges, the characters used by Priem to distinguish *mokattamensis* from other species and to link the vomers with the splenials of *mokattamensis*. The vomers of this species are closest in appearance to *P. pachyrhinus* Egerton but as Priem points out the median teeth of *P. pachyrhinus* have even more arched anterior borders. The first lateral teeth in *pachyrhinus* are oval but are slightly wider at the anterior end, not the posterior end. The vomers of *mokattamensis* differ from *P. zeaformis* and *P. jonesae* in all the characters listed in the diagnoses of the latter two species.

Pycnodus munieri Priem
Figs 25h–j, 28

1902 *Pycnodus munieri* Priem: 44; fig. 1. Eocene, Couiza (Aude), France.
1908 *Pycnodus munieri* Priem; Leriche: 7; pl. 1, fig. 4. Ypresian, Fabrezan (Aude), France.

This species is known by two fairly complete vomers, the one figured by Leriche being described as juvenile. The vomers have ovoid median teeth, slightly arched in front and with a straight posterior border. The first lateral teeth are subtriangular with a wider posterior end and have a concave inner anterior border. The inner corners of the first lateral teeth tend to extend inwards between the median teeth. The second lateral teeth are oval and aligned with the first lateral teeth in Leriche's specimen. In Priem's specimen, however, the second lateral teeth are aligned with the first lateral teeth on one side but alternate with them on the other, showing that this character can vary in an individual as well as within a species. In the Mali fauna two specimens, BMNH P.60635 (Figs 25j, 28) and P.60922, are identified as *P. munieri*. They especially resemble the specimen figured by Leriche (Fig. 25h) and have all the characters described for *P. munieri*.

P. munieri differs from *P. variabilis* and *P. pachyrhinus* in the shape of the first lateral teeth and in having more oval median teeth. The first lateral teeth of *P. pachyrhinus* are wider at the anterior end, not the posterior end as in *P. munieri*. *P. munieri* differs from *P. mokattamensis* in having slightly wider median teeth and no crenulations around the teeth. *P. munieri* differs from *P. zeaformis* and *P. jonesae* in all characters mentioned in the diagnoses (p. 7).

Pycnodus lemellefensis Savornin
Fig. 25g

1915 *Pycnodus lemellefensis* Savornin: 371; fig. 2. Lower Eocene, Bordj-Redir, Algeria.

The species is represented by one medium-sized vomer (average width of median teeth 18 mm). The median teeth are ovoid and relatively wider than those of *mokattamensis* and *variabilis*. Savornin said that his specimen differed from other Tertiary species in having second lateral teeth aligned with the first lateral teeth and not alternating with them. As noted above, both states of this character occur in one individual of *P. munieri*. Savornin's other main reason for erecting his new species is that the median teeth have a notch in the anterior outer edge. However, from his figure this character occurs on one side only on two out of five median teeth. It is a character common in pycnodont dentitions that where two teeth grow closely together their shape may be altered. In all respects the vomer resembles those of *P. munieri* and should be synonomized with it. It differs from *P. zeaformis* and *P. jonesae* in all characters listed in the diagnoses of those species.

Pycnodus legrandi Savornin
Fig. 25f

1915 *Pycnodus legrandi* Savornin: 374; fig. 3. Lower Eocene, Tocqueville, Algeria.

An incomplete vomer is the only specimen of this species. Savornin differentiated it from *lemellefensis* because the tooth-bearing surface of the vomer of *legrandi* is biangular when viewed from behind, and not regularly arched. This character, however, is variable within the Mali species, and can be affected by wear. The vomer is otherwise very similar to those of *lemellefensis* and *munieri* and *P. legrandi* should be synonymized with *P. munieri*.

Pycnodus thamallulensis Savornin

1915 *Pycnodus thamallulensis* Savornin: 375; fig. 4. Lower Eocene, Tocqueville, Algeria.

This species is known by one very incomplete vomer. The median tooth is rectangular and so differs from those of Savornin's other specimens in having a less arched anterior border. The first lateral teeth, of which only two are preserved, are regularly oval and have their longest axes at 45° to that of the median tooth. Savornin compares this specimen to *P. munieri* and notes a similarity except that the first lateral teeth are oval and there is a large space (5 mm) between the median and first lateral rows. In these respects the specimen closely resembles *P. tattami* White.

Pycnodus savini Priem
Fig. 26a

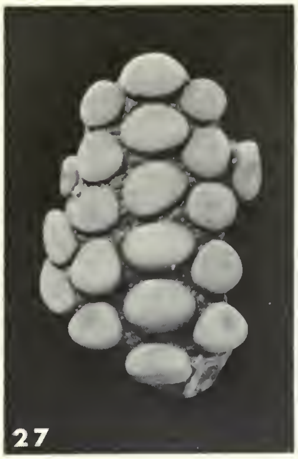
1902 *Pycnodus savini* Priem: 46; fig. 2. Middle Eocene, Villespy (Aude), France.

Priem described this species from Aude on an incomplete vomer of larger size (average width of median teeth 22 mm) than *P. munieri* (average width of median teeth 11 mm). The specimen differs from all other Tertiary species in having oval median teeth with slightly pointed outer ends. The median teeth also tend to have a slightly concave anterior border and a convex posterior one. The median teeth are unlike those of other species except *P. zeaformis* and *P. jonesae* in that they are about twice as wide as long. However, the teeth of the first and second lateral rows are oval and orientated respectively at about 60° and 90° to the median teeth. In these respects *P. savini* differs from *P. zeaformis*. It differs from *P. jonesae* in the shape of the median teeth. Priem's view that this specimen represents a distinct species seems justified.

Pycnodus pachyrhinus Egerton
Figs 25l, 29

1877 *Pycnodus pachyrhinus* Egerton: 54; pl. 4, figs 1, 2. Ypresian, Kent, England.
1895 *Pycnodus pachyrhinus* Egerton; Woodward: 278. Ypresian, Kent, England.

The species is based on an almost complete vomer, BMNH P.610. The specimen resembles *P. mokattamensis* in having median teeth with strongly arched anterior borders and straight posterior ones. The first lateral teeth are oval but slightly wider at the anterior end. The second lateral teeth are also oval when unworn. In these respects it differs from *mokattamensis* and *munieri*. Woodward identified a worn vomer, BMNH P.170, as *P. pachyrhinus*. This specimen is similar to the holotype but has more oval median teeth. However, the first lateral teeth are so similar to those of the holotype that BMNH P.170 is probably correctly identified as *P. pachyrhinus*. *P. pachyrhinus* differs from *P. zeaformis* and *P. jonesae* in all characters mentioned in the diagnoses. As Egerton said, there is no evidence to indicate whether *P. pachyrhinus* is a vomer of *P. toliapicus* or of *P. bowerbanki*, both of which are also found in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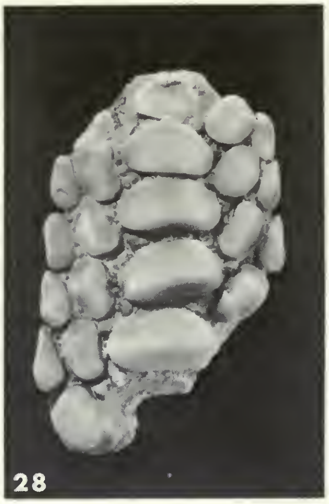
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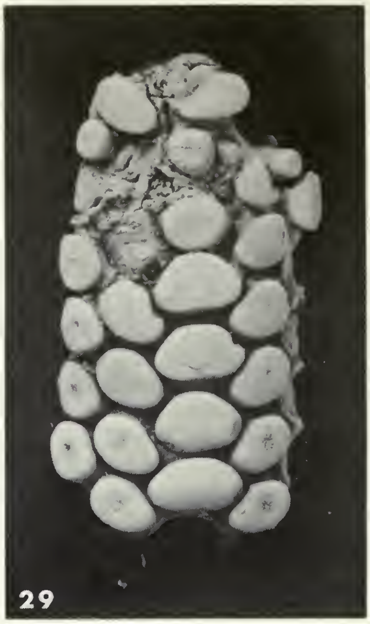
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Figs 27–29 Vomers of *Pycnodus* species. Fig. 27, *P. variabilis*, TGE 625, ×2. Fig. 28, *P. munieri*, BMNH P.60635, ×2. Fig. 29, *P. pachyrhinus*, holotype BMNH P.610, ×1.

the London Clay, or of some other species, therefore the name *pachyrhinus* should remain valid.

Pycnodus toliapicus Agassiz
Fig. 25k

1966 *Pycnodus toliapicus* Agassiz; Casier: 104; pl. 11, fig. 5. Red Crag (London Clay derived), Suffolk, England.

Casier described a vomer, BMNH P.10121, as *P. toliapicus*. He stated that it is similar to BMNH P.170 and BMNH P.610 (both *P. pachyrhinus*) and suggested that *P. pachyrhinus* should be synonymized with *P. toliapicus*. The proportions of the teeth of BMNH P.10121 and *P. pachyrhinus* are similar but the tooth shape is very different. BMNH P.10121 resembles *P. munieri* much more closely than it does *P. pachyrhinus* in that the median teeth in BMNH P.10121 are more or less ovoid, and the first lateral teeth trapezoidal with a wider posterior end and a concave inner anterior border in some teeth. BMNH P.10121 is probably a specimen of *P. munieri*; hence *P. toliapicus* would still be known only by splenial dentitions.

Two other *Pycnodus* species are known from the Tertiary, *Pycnodus apodus* (Volta) (= *P. platessus* Agassiz), and *Pycnodus gibbus* Agassiz. These are based on complete fishes from the Middle Eocene of Monte Bolca, Italy. In these species the dentitions are extremely small. There are few teeth in each row and these decrease rapidly in size anteriorly so that the anterior teeth in all rows are barely wider than long. The posterior teeth in the splenials are oval in the medial and first lateral rows but circular in the second lateral row. The vomerine teeth are poorly known but are also very small and decrease rapidly in size forwards. I do not believe any other described species is synonymous with either of these two species, because of the small size of the dentitions and the narrowness of the second lateral teeth on the splenials.

Conclusion

The above survey leads me to suggest that the number of Tertiary *Pycnodus* species known only by splenials or vomers should be reduced.

The following species should be considered valid.

Pycnodus bowerbanki Egerton, splenials
Pycnodus jonesae sp. nov., vomers.
Pycnodus maliensis sp. nov., splenials
Pycnodus mokattamensis Priem, splenials and vomers
Pycnodus munieri Priem, vomers. This species to include *P. lemellefensis* Savornin, *P. legrandi* Savornin and Casier's (1966) *P. toliapicus* specimen, BMNH P.10121.
Pycnodus pachyrhinus Egerton, vomers
Pycnodus pellei Priem, splenials
Pycnodus savini Priem, vomer
Pycnodus tattami White, vomers
Pycnodus thamallulensis Savornin, vomer. This species may be the same as *P. tattami.*
Pycnodus toliapicus Agassiz, splenials. This species to include *Periodus koenigii* Agassiz, Stromer's (1905) specimens St5 and M1, *P. variabilis* var. *togoensis* Stromer, *P. vasseuri* Savornin, and *P. praecursor* Dartevelle & Casier, splenials only.
Pycnodus variabilis Stromer, vomers and splenials. This species to include Stromer's (1905) specimen St2, White's (1935) specimen BMNH P.18826, and *P. praecursor* Dartevelle & Casier, vomers only.
Pycnodus zeaformis sp. nov., vomers.

The abundant *Pycnodus* material from Mali has proved useful in showing the variation that can occur within a species, so clarifying the features that can best be used for diagnosis. Tooth shape can vary within *Pycnodus* species, and single teeth or very incomplete vomers or splenials cannot be identified with any certainty. The relative proportions of the teeth in the various rows can be a useful diagnostic feature but this must be combined with overall tooth shape, especially in the vomers.

Table 3 shows the stratigraphical range of the Tertiary *Pycnodus* species discussed previously. Although the pycnodonts are common in the phosphate deposits in Mali they are not useful for dating purposes. Three species found in Mali (*P. variabilis, P. munieri* and *P. bowerbanki*) are known elsewhere from the Landenian to the Lutetian. This is the range of ages that has also been suggested for the Mali phosphates (Lowest Eocene by R. T. Moody and Middle Eocene by H. Radier, see Introduction), so the range of these *Pycnodus* species does not help to resolve the problem of the age of the Mali phosphates.

The Mali specimens do illuminate the problem of tooth replacement in pycnodonts. In these specimens the main difference between large and small dentitions of the same species is that the anterior region of the large dentitions is covered in small round irregularly-arranged teeth instead of the normal elliptical teeth arranged in rows. According to Thurmond (1974: 110) and Woodward (1895: 194) pycnodont dentitions grew by the addition of new and larger teeth at the posterior end of the vomer and splenial. The anterior teeth were worn until they were no longer functional and then lost (whether they were shed or resorbed is not stated). Thurmond and Woodward also said that there does not appear to be any replacement of individual teeth. This would mean that the anterior teeth are the oldest, and therefore the small, round, anterior teeth in the large Mali dentitions would be those that had been functional in the juvenile and should show most wear. Woodward (1893: 433) believed that juveniles would have had small round teeth. However, as stated above the small specimens from Mali have the characteristic regularly-arranged elliptical or oval teeth and very few small round teeth. In the larger dentitions the most anterior normal-shaped teeth show more wear than the posterior ones but the small round teeth in front of them show little or no wear. In many large specimens the most anterior elliptical teeth are so worn that the pulp cavity is exposed. In some, part of the tooth has disappeared entirely (apparently by resorption rather than wear) and small round teeth can be

Table 3 Stratigraphical distribution of Tertiary *Pycnodus* species.

	PALAEOCENE		LOWER EOCENE	MIDDLE EOCENE
	Montian	Landenian	Ypresian	Lutetian
P. variabilis				+
P. v. var. *togoensis*		+		
P. vasseuri			+	
P. praecursor	+ · · · · · · ?	· · · · · · +		
TGE 625			+ · · · · · ?	· · · · +
P. pellei			+	
P. mokattamensis				+
P. pachyrhinus			+	
P. tattami		+		
P. thamallulensis			+	
P. munieri			+	
BMNH P.60635			+ · · · · · ?	· · · · +
BMNH P.10121			+	
P. lemellefensis			+	
P. legrandi			+	
P. toliapicus			+	
P. koenigi			+	+
P. savini			+	
P. bowerbanki			+	
GAO 7			+ · · · · · ?	· · · · +
BMNH P.60917			+ · · · · · ?	· · · · +
P. maliensis			+ · · · · · ?	· · · · +
P. zeaformis			+ · · · · · ?	· · · · +
P. jonesae			+ · · · · · ?	· · · · +

observed within the outline of the original ellipse (e.g. see tooth marked *a* in Fig. 13). No small teeth have been observed within the pulp cavity of intact teeth. Examination of numerous large and small vomers and splenials from Mali gives the impression that the dentitions grew by the addition at the rear of new, larger elliptical teeth but also that the juvenile pattern of regular elliptical teeth was progressively replaced from the front by irregularly-arranged small round teeth. This replacement was not direct as a phyllodonts (Estes 1969) but appears to have been interstitial with resorption of part of the pre-existing worn tooth. Sections of dentitions of *Pycnodus* and other pycnodont genera have not yet shown tooth replacement conclusively, but future work involving sectioning and possibly X-raying of the Mali specimens may do so. The phenomenon of small round irregularly-arranged teeth is common in *Pycnodus* species but rare in other pycnodont genera. However, I have observed it in vomers and splenials of the genera *Gyrodus, Coelodus, Eomesodon* and *Macromesodon*. The whole question of tooth replacement in pycnodonts merits further study.

Acknowledgements

I wish to thank Dr P. Forey and Dr C. Patterson (BMNH) for their patience and help whilst writing this paper. I also thank Dr R. T. Moody (Kingston Polytechnic) and Mr C. A. Walker (BMNH) for information on the stratigraphy of Mali and North Africa and, with the other members of the 1981 expedition, for their enthusiasm in collecting the specimens. I also thank Dr Eric Buffetaut (Laboratoire de Paléontologie, Paris) for the loan of the material from that institution, and the British Museum (Natural History) Photographic Unit for the photographs.

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**Bulletin of the
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C. H. C. Brunton

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The Geology Series is edited in the Museum's Department of Palaeontology
Keeper of Palaeontology: Dr H. W. Ball
Editor of the Bulletin: Dr M. K. Howarth
Assistant Editor: Mr D. L. F. Sealy

ISBN 0 565 07001 0
ISSN 0007–1471

British Museum (Natural History)
Cromwell Road
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Vol 38 No 2 pp 27–130

Issued 26 July 1984

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Synopsis

The description of acid-developed silicified brachiopods from Viséan limestones near Derrygonnelly, County Fermanagh, Ireland, is completed. The taxa belong to the Rhynchonellida, including the Stenoscismatacea, the Spiriferida and the Terebratulida. New taxa are *Propriopugnus* gen. nov., type species *'Pugnax' pugnus* (Martin 1809); *Cyrtina hibernica* sp. nov.; *Minythyra lopha* gen. et sp. nov. and *M. ernea* gen. et sp. nov. in the new family Verneuiliidae; *Cryptonella minranensis* sp. nov.; *Girtyella carrickensis* sp. nov.; *Alwynia reidi* sp. nov. and *Beecheria treakensis* sp. nov. Lectotypes are selected for four J. Phillips species, *Terebratula radialis, Spirifer ovalis, S. integricosta* and *S. insculpta*; also of *Terebratula ulothrix* de Koninck, *Spirifer carlukensis* Davidson and *Merospirifer insolita* Reed. Neotypes are selected for *Terebratula trilatera* de Koninck, *Spirifer deroissyi* Léveillé, *Tylothyris laminosa* (M'Coy) and *Verneuilia oceani* (d'Orbigny).

The excellence of the silicified material allows detailed descriptions of internal features to be given, and the morphological changes resulting from growth are discussed. Study of the terebratulids points to a much wider diversity of species in British Viséan rocks than has hitherto been recorded. The composition of the complete fauna of brachiopods is presented.

Introduction

This paper describes the third and last part of the brachiopod faunas collected principally from two Asbian (D_1 or B_1), Viséan localities in Co. Fermanagh at the Sillees river and at Carrick Lough (Fig. 1), and extracted by acid development. Brief descriptions of the localities and their geological settings have been published (Brunton 1966*a*, 1968; Tavener-Smith 1973), but a more

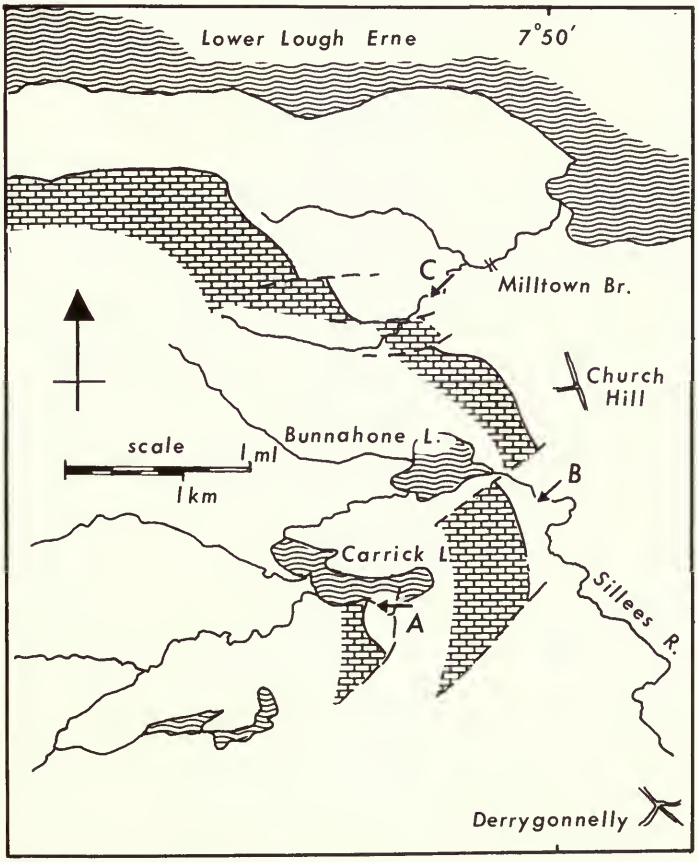
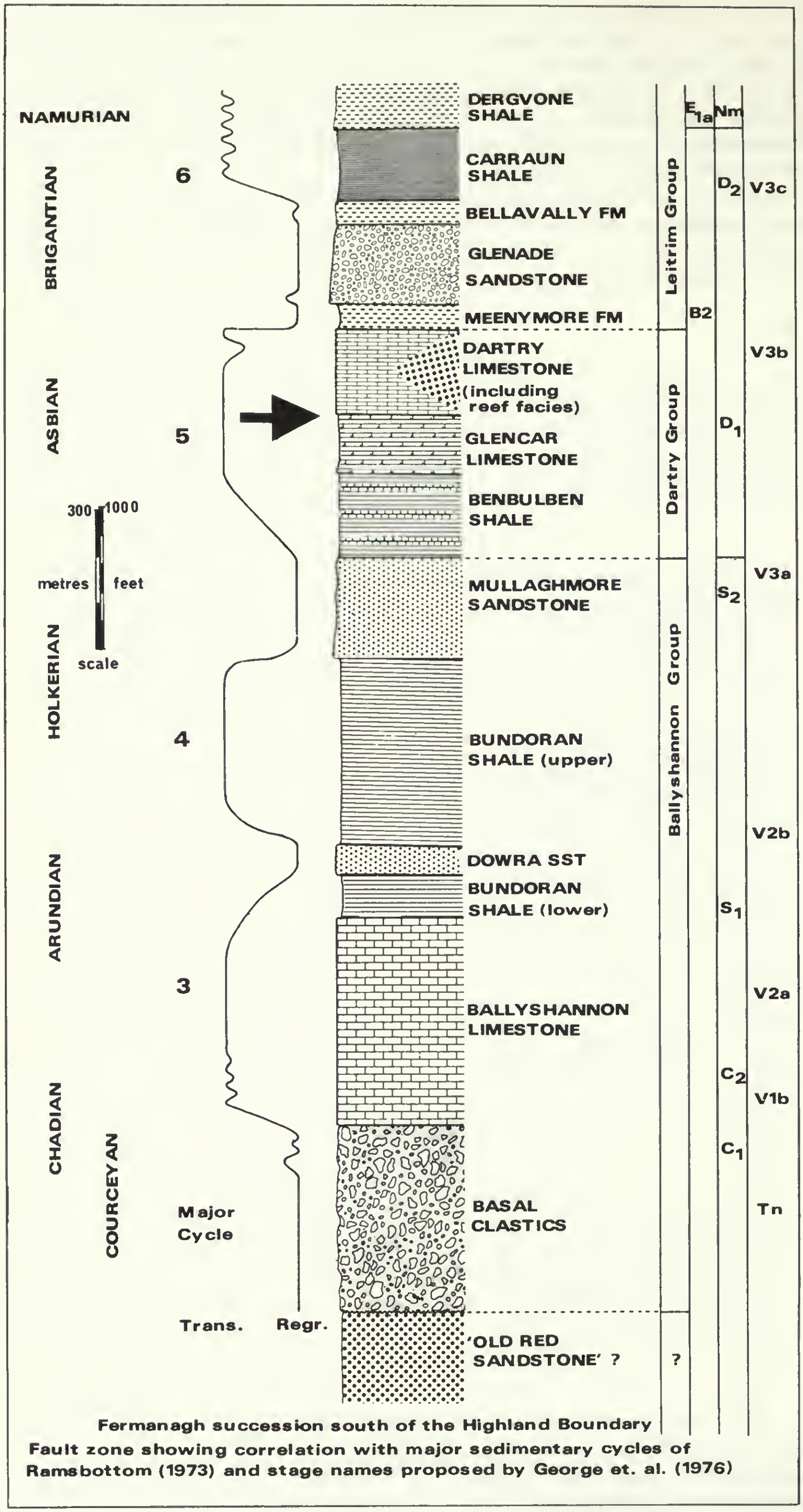


Fig. 1 Map of part of County Fermanagh showing the collecting localities at Carrick Lough (A), near Bunnahone Lough (B) and near Milltown Bridge (C). The arrows also indicate the direction of dip. The small brick symbol indicates areas of lower Dartry Limestone and thus shows its basal junction with the Glencar Limestone. (For the general geological setting see Brunton & Mason 1979).


NAMURIAN
BRIGANTIAN
ASBIAN
HOLKERIAN
ARUNDIAN
CHADIAN
COURCEYAN
300
1000
metres
feet
scale
6
5
4
3
Major Cycle
Trans.
Regr.
DERGVONE SHALE
CARRAUN SHALE
BELLAVALLY FM
GLENADE SANDSTONE
MEENYMORE FM
DARTRY LIMESTONE (including reef facies)
GLENCAR LIMESTONE
BENBULBEN SHALE
MULLAGHMORE SANDSTONE
BUNDORAN SHALE (upper)
DOWRA SST
BUNDORAN SHALE (lower)
BALLYSHANNON LIMESTONE
BASAL CLASTICS
'OLD RED SANDSTONE' ?
Leitrim Group
Dartry Group
Ballyshannon Group
?
E_{1a}
B2
Nm
D_2
D_1
S_2
S_1
C_2
C_1
V3c
V3b
V3a
V2b
V2a
V1b
Tn

Fermanagh succession south of the Highland Boundary Fault zone showing correlation with major sedimentary cycles of Ramsbottom (1973) and stage names proposed by George et. al. (1976)

Fig. 2 The stratigraphical succession in County Fermanagh showing the level, in the Asbian, from which the bulk of the faunas were collected. (From Brunton & Mason 1979).

detailed account of the geology of west Fermanagh was presented by Brunton & Mason (1979). The stratigraphical position of the collection localities is shown in Fig. 2; the Asbian (B_1) age has recently been supported by Mitchell & Mitchell (1982).

The two previous Bulletins (Brunton 1966*a*, 1968) covered the inarticulates, orthids and strophomenoids, a total of 31 species. Here the rhynchonellids, spire-bearers and terebratulids are described, adding 24 species (plus an extra productacean) to the total of 56 recognized brachiopod species. In this study a greater use has been made of comparative material from areas beyond Fermanagh, found to be necessary in determining and decribing more accurately some taxa; it also includes the selection of lectotypes for some well-established species. While many of the brachiopods described in Phillips' (1836) important study of the geology of Yorkshire remain without established type specimens, those of his species recognized in the Fermanagh faunas have their lectotypes chosen and figured here, pending a major review of the Yorkshire material still in progress. Two species have already been described, principally from non-silicified material; the endopunctate rhynchonellid *Tretorhynchia trilatera* (de Koninck) (Brunton 1971), and the spiriferid *Fusella rhomboidea* (Phillips) (Brunton & Rissoné 1976).

Because the faunas have been extracted from the limestones by acid digestion the numbers of specimens are large; commonly a species is represented by hundreds of individuals. Also the range in size of specimens commonly covers much of the species' inferred growth, allowing information to be given for the first time on their variability and growth changes. Some species are represented by large numbers of small specimens, which probably indicate the population structure more closely than would specimens collected by traditional methods of cracking out from the rock.

Silicification

The brachiopods from the Fermanagh localities are commonly incompletely silicified, especially if originally thick-shelled, but the silicification is fine in its replacement of the original shell material and usually replicates the major shell fabrics. Thus endopunctuation and pseudopunctation are commonly recognizable, as seen both at the surface and in broken sections of shell. Similarly, on some specimens, a representation of internal shell mosaic can be seen. These features show that the process was a fine replacement of calcite by silica, not one of total shell solution, followed by silica infilling. The details of external and internal morphologies preserved by silica show that the process started at the surface of the fossils and progressed inwards, following existing fabrics. Some silicified shells are slightly crushed, as if sediment compaction cracked them prior to silicification; silica connects the broken edges. The silicified specimens have, however, also been cracked by regional jointing and it seems likely that silicification occurred during, or closely following, lithification of the rock.

The silicification process was somewhat selective, in that large calcite crystals from crinoids are seldom silicified sufficiently to withstand acid extraction. However, silicification has occurred in the fully calcitic shells of both brachiopods and molluscs as well as in the shells of aragonitic molluscs. Schmitt & Boyd (1981) described patterns of silicification in some Permian brachiopods and bivalves from Wyoming, and Holdaway & Clayton (1982) described late Cretaceous silicified brachiopods from Devon and suggested models for the morphologies of silica they recognized. The Fermanagh brachiopods fall into pattern V of Schmitt & Boyd, which is equivalent to the 'fine textural replacement' of Holdaway & Clayton. Rarely, but slightly more commonly at Boho Quarry, replacement is by beekite rings, or pattern IV of the American authors. Briefly, the Holdaway & Clayton model suggests that the aerobic decay of organic matter raised the partial pressure of carbon dioxide in a restricted microenvironment, and that if silica was in plentiful supply it was precipitated, seeding onto existing shell fabric boundaries, as the calcite was progressively dissolved. Where silica was in limited supply beekite silicification resulted. These authors, and others, have pointed to the differences in dissolution between calcitic and aragonitic shells, the latter tending to be dissolved more completely than the former before the growth of the quartz crystals. This leads to a coarser form of silicification in aragonitic shells, so that many of the Fermanagh molluscan shells are preserved in silica which does not reproduce the original morphologies as faithfully as in the fully calcitic brachiopod shells. Silicification patterns I to IV of Schmitt & Boyd (1981) result from quartz growths into voids resulting from the dissolution of aragonitic or mixed aragonitic plus calcitic shell fabrics.

Systematic palaeontology

Unless otherwise explained, the classification and terminology used here are as in the *Treatise on Invertebrate Paleontology,* **H**, Brachiopoda (Williams *et al.* 1965). Descriptive terms for the outline shapes of shells are as suggested by the Systematics Association committee for descriptive biological terminology (Exell & Lewis 1962), and notations in the synonymy lists follow Matthews (1973). Almost all the specimens described and mentioned are in the collections of the British Museum (Natural History), but some are in the University Museum, Oxford (E registration numbers), the collections of the British Geological Survey (IGS registration numbers), the National Museum of Ireland, Dublin (Griffith collection), or l'Institut Royal des Sciences Naturelles de Belgique, Brussels (IG registration numbers).

All the silicified specimens from Fermanagh illustrated here came from the Sillees river locality (14/4B), unless otherwise stated in the figure explanation.

Order **RHYNCHONELLIDA** Kuhn 1949

Superfamily **RHYNCHONELLACEA** Gray 1848

Family **PUGNACIDAE** Rzhonsnitskaya 1956

Genus ***PROPRIOPUGNUS*** nov.

TYPE SPECIES. *Conchyliolithus Anomites pugnus* Martin 1809 (see Muir-Wood 1956).

DIAGNOSIS. Strongly folded pugnacidae with few ribs originating in posterior half, but only fully developed anteriorly. Dental plates short. Small umbonal septalium and wide subhorizontal outer hinge plates with medially separated crural bases.

NAME. Latin *proprius* = genuine, + *pugnus* = fist. Masc.

DISCUSSION. The type species has been assigned in recent years to *Pugnax* Hall & Clark 1893, with *P. acuminatus* (J. Sowerby) as type species. Interiors of *P. acuminatus* were essentially unknown till Schmidt (1965) illustrated serial sections, which were repeated in the *Treatise* (Williams *et al.* 1965: H574) to illustrate *Pugnax*. From those serial sections it is clear that the Fermanagh specimens differ sufficiently to be removed from *Pugnax*. In order to check the differences I have ground the umbones of a specimen *P. pugnus* from the Dinantian limestones of Bolland (BM(NH), B371) which externally resembles the holotype very closely. The internal structures are as in the Irish silicified specimens.

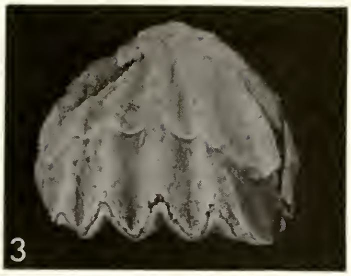
In his study of Mississippian rhynchonellids Weller (1910) illustrated some serial sections called *Pugnax pugnus* (Martin) from the 'Mountain limestone fauna of Ireland'. These sections are good representations of the species, but he did not relate them to the type species, *P. acuminatus*. At that time (1910) Weller erected *Pugnoides* and *Shumardella*; the former tends to be smaller than either *Pugnax* or *Propriopugnus* and is more completely ribbed, while the latter resembles the new genus externally. Internally *Shumardella* differs from the new genus in its strong dental plates and tall persistent dorsal median septum.

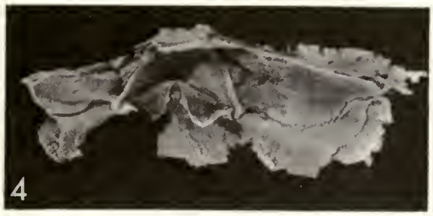
The Tournaisian genus *Ningbingella* Roberts 1971 from north-western Australia resembles *P. pugnus* externally, but internally the Australian genus has a septalium and long, well-defined dosal median septum which, anteriorly, continues to support the socket ridges and hinge plates.

Propriopugnus pugnus (Martin)

Figs 3–4

v* 1809 *Conchyliolithus Anomites (pugnus)* Martin: pl. 22, figs 4, 5.
v* 1951 *Pugnax pugnus* (Martin) Muir-Wood: pl. 4, figs 3a–c.





Figs 3, 4 *Propriopugnus pugnus* (Martin) from the Sillees river collections. Fig. 3, an almost complete specimen viewed dorsoposteriorly. BB63645, ×2. Fig. 4, interior of the umbones of an incomplete specimen viewed posteriorly; the ventral valve, with its dental plates, is uppermost. BB63646, ×4.

DIAGNOSIS. In posterior view very broadly obovate. Anterior commissure strongly uniplicate, with three or four ribs within ventral sulcus and up to two smaller ribs on each flank. Short dental plates, close to valve surface; low short dorsal median septum supporting a small septalium in tip of umbo.

LOCALITY AND HORIZON. Martin's original information is 'Carboniferous Limestone – Derbyshire'. A detailed locality cannot be provided, but the age is probably mid to upper Viséan.

HOLOTYPE. Martin's figured specimen is in the Sowerby Collection, BM(NH) B61451, as *Rhynchonella pugnus* Martin. This was recognized as holotype by Muir-Wood (1951) in connection with her submission to the International Commission on Zoological Nomenclature, Opinion 419 (Muir-Wood 1956), upholding Martin's authorship for the species.

DISCUSSION. Sowerby (1825: 156), in discussing Martin's specimen, wrote that its blunt form arose from distortion caused by several fractures. The specimen is certainly fractured but remains essentially undistorted. It is a feature of this species that, once a shell grew to between 15 and 20 mm long, growth directions altered so that the valve margins opposed one another. In this way additional growth thickened the depth of the shell rather than adding much to its length. Parkinson (1954) did not discuss this aspect of growth in his comparative studies of *Pugnax* species. The dimensions of the holotype (l = 24·5 mm, w = 35·4 mm, th = 25·5 mm) differ only very slightly from those of the large specimen (B61218) figured by Sowerby (1825: pl. 497, figs 1).

The species is here transferred from *Pugnax* to *Propriopugnus* on account of its internal characteristics and because the type species of *Pugnax, P. acuminatus* (J. Sowerby) (lectotype in the BM(NH), B61235), differs from *pugnus* in possessing a very high, pointed, fold and lacking any well-developed ribs.

The species is represented in the acid-developed faunas from Co. Fermanagh by only a few fragmentary specimens; one incomplete specimen shows the umbonal regions (Fig. 4). Because fragmentation could have resulted from the acid development, these fragments could represent four or five shells as originally preserved in the rock. Two of the more incomplete specimens were filled by crystalline quartz rather than sediment. It seems likely, therefore, that these shells at least were complete at the time of their burial. However, the partially crushed state of some specimens suggests a degree of fragmentation prior to the acid development and it might be that these specimens were carried into the collection site, on the Sillees river, prior to burial.

In addition the species is found rarely in the fossiliferous limestones flanking the 'reefs' which developed within the overlying Dartry Limestone.

Genus *PLEUROPUGNOIDES* Ferguson 1966

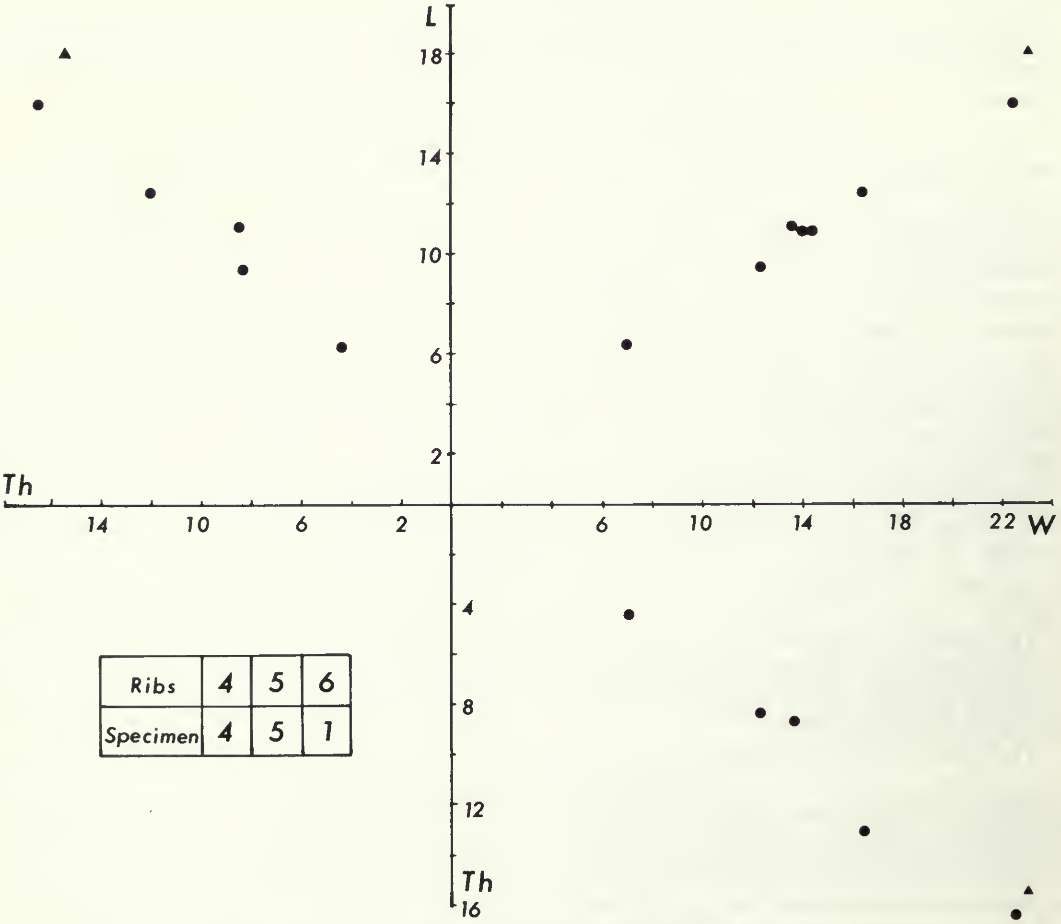
TYPE SPECIES. *Terebratula pleurodon* Phillips (1836: 222; pl. 12, figs 25, 26), by original designation of Ferguson (1966: 354).

Pleuropugnoides pleurodon (Phillips)
Figs 5–8

DIAGNOSIS (emended). Wide rhynchonelliform shape with strongly serrated uniplicate commissure. Strong ribs originating at umbos, commonly 4 or 5 in ventral sulcus. Dorsal median septum extending anteriorly of sockets, high posteriorly and forming short septalium.

LECTOTYPE. Ferguson (1966) selected as lectotype the specimen figured by Phillips (1836: pl. 12, figs 25, 26), which was collected from Bolland and is in the Gilbertson Collection of the BM(NH), B361. It was refigured by Ferguson when he redescribed the species (1966: pl. 23, figs 1–3).

MATERIAL. The species is poorly represented in the silicified faunas, there being only ten reasonably complete shells from which measurements could be taken. Partially preserved



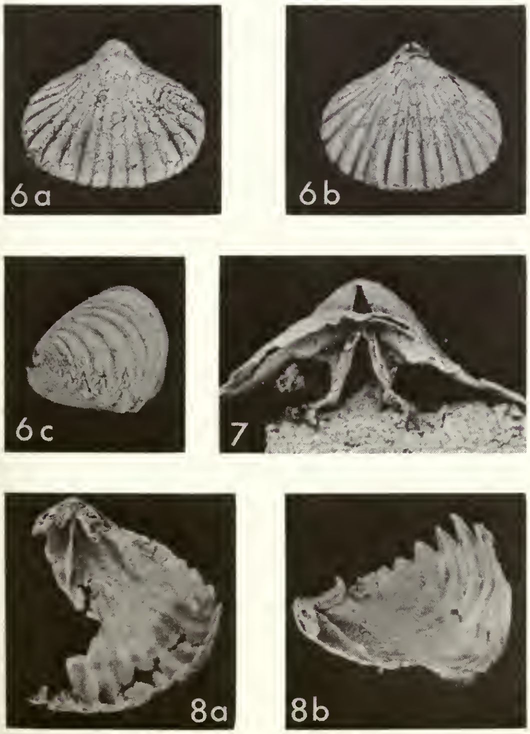
Ribs	4	5	6
Specimen	4	5	1

Fig. 5 *Pleuropugnoides pleurodon* (Phillips). Length, width and thickness plots of seven specimens from Co. Fermanagh, plus the lectotype (▲) from Bolland, Yorkshire. Only five of the silicified specimens could be measured for thickness. The table shows the number of ribs counted in the sulcus of ten silicified specimens (cf. Ferguson 1966: 363, table 1).

umbonal regions of two specimens allow some additional information to be given here beyond that of Ferguson's description.

Discussion. The length, width and thickness of the Fermanagh specimens fit closely to those dimensions given for the species by Ferguson. Within the ventral sulcus 4, 5 and 1 specimens have 4, 5 and 6 ribs, whilst the lectotype is atypical in having only 3 ribs in its sulcus. The number of these ribs is a variable characteristic, as can be seen from the Gilbertson Collection specimens (from which the lectotype was chosen), but 4 or 5 ribs is normal (Fig. 5; see also Ferguson 1966: table 1 and Parkinson 1969: table 6). Several of the silicified specimens clearly show that the dorsal median septum extended for up to one-third of the total valve length, well anteriorly of the crural bases (Fig. 8). The septum extends anteriorly to separate the posterior regions of the paired and slightly depressed adductor muscle scars. Posterolaterally of these scars the valve floor is marked by irregular depressions and protuberances, which probably indicate the positions of the genital sacs, as in the living *Hemithyris*. Also, as in living rhynchonellids, the sockets are transversely striated. However, the cardinal process and crura differ considerably from most living representatives. In *P. pleurodon* the dorsal attachment for the diductor muscles is indistinct and seems to have been no more than a roughened area on the apex of the hinge plate; this plate is fused posteriorly with the median septum. The crura extend anteroventrally and their slightly concave blade-like surfaces are orientated at first medially, but anterodorsally towards their tips. The morphology of the cardinalia of these Carboniferous species is more akin to that of the living genera *Compsothyris* or *Hispanirhynchia* than to that of the well-known *Hemithyris* or *Notosaria*.

The somewhat broken condition of the silicified specimens, together with the lack of young individuals and signs of infestations by boring organisms, indicate that they may have remained dead on the sea floor for some time before burial. Closely comparable specimens are locally abundant from 'reef' flanking limestones in the overlying strata. These commonly have six costae in the ventral sulcus but otherwise would seem to be identical to the rare silicified material collected from both the Sillees River and Carrick Lough localities. It seems probable that these



Figs 6–8 *Pleuropugnoides pleurodon* (Phillips). Fig. 6, a young shell in ventral, dorsal and lateral aspects. BB63660, ×2. Fig. 7, the umbonal region of an incomplete shell showing the underside (dorsal surfaces) of the sockets, hinge plates and crura, and the pedicle aperture in the ventral valve. BB63662, ×4. Fig. 8, an incomplete dorsal valve showing the interior viewed dorsally and laterally. BB63661, ×3.

two forms of *Pleuropugnoides* are closely related, but the silicified specimens are sufficiently distinctive to show that they were not derived from some contemporaneous 'reefal' locality.

Superfamily **RHYNCHOPORACEA** Muir-Wood 1955

Most authors assign the rhynchoporaceans to the rhynchonellids on account of their general morphology. It should be noted, however, that Cooper & Grant (1976: 2651) do not assign the superfamily to an order, when describing their abundant silicified Permian species from west Texas, in their belief that the endopunctation of rhynchoporaceans is of sufficient importance to exclude them from the Rhynchonellida (see Cooper & Grant 1976: 1923). Their view would lead to major brachiopod reclassification. My opinion is that the endopunctate condition in brachiopods is one that appeared and reappeared in several groups as the result of genetical changes, as it were switching on or off the coding for the growth of mantle caecae, which led to the endopunctate shell condition. If this were so then I feel it would be better to retain the otherwise similar rhynchoporaceans within the Rhynchonellida.

Family **RHYNCHOPORIDAE** Muir-Wood 1955

Genus ***TRETORHYNCHIA*** Brunton 1971

Diagnosis. Outline subtriangular, profile somewhat flattened with thickness just over half width. Anterior commissure rectimarginate. Eighteen to twenty-two strong angular costae on dorsal valves, ventral valves with median costa. Dorsal median septum and wide septalium with vertically disposed blade-like crura. Dental plates short.

This genus was established by Brunton (1971) with type species *Terebratula trilatera* de Koninck from the Viséan of Belgium. The species was described utilising solid specimens from the Viséan 'reefal' limestones of Derbyshire and Staffordshire as well as from other localities in the north–central area of England, north Wales and a possible subspecific variant from the south of Ireland. Internal morphology was based on information from serial sections. The acid-developed Fermanagh faunas contain several broken adults and approximately 35 juvenile specimens, mostly less than 3 mm long. Well-preserved valve interiors are available and although it remains unnecessary to emend the generic diagnosis of 1971 further information can now be presented.

Tretorhynchia trilatera (de Koninck)
Figs 9–20

1843 *Terebratula trilatera* de Koninck: 292; pl. 14, figs 7a–d.
v. 1887 *Rhynchonella trilatera* (de Koninck) de Koninck: 50; pl. 16, figs 68–83.
1971 *Tretorhynchia trilatera* (de Koninck) Brunton: 99; pls 11, 12.

Diagnosis. Outline approximately equilateral triangular with rounded anterolateral margins. Flattened posterolateral flanks. Costae strong, angular, commonly 18–22 on dorsal valves, median rib on ventral valves. Endopunctate.

Neotype. That figured by de Koninck (1887: pl. 16, figs 69–75) in the Brussels Museum, no. IG 2738b (Brunton 1971: 99) is here selected neotype.

Description. The silicified material largely supports the description given in 1971 but allows the internal morphology to be described more fully from direct evidence rather than from the sets of serial sections used previously.

Within the ventral valve the dental plates converge slightly from below the teeth onto the valve floor (Figs 14, 18), and a faint median ridge, or myophragm, extends anteriorly from between their bases. The teeth are somewhat recurved and crytomatodont (Jaanusson 1971), typical of the Rhynchonellida (Figs 9a, 20).

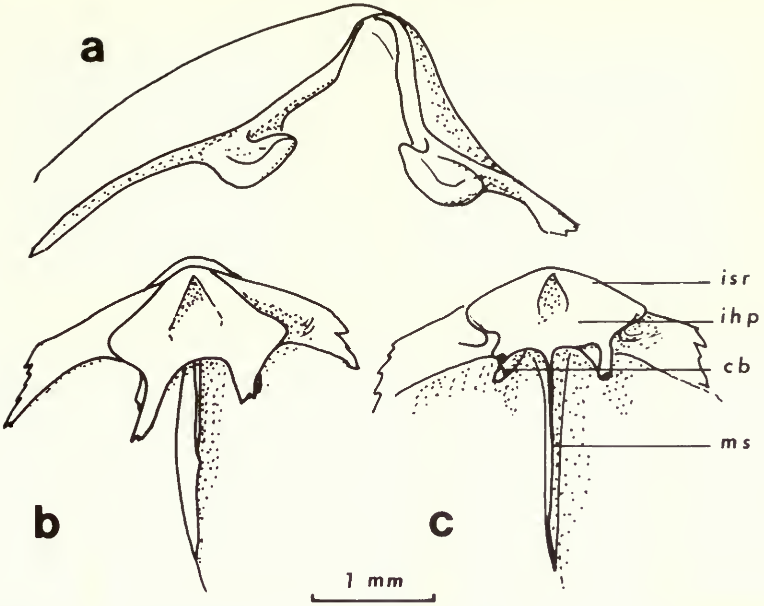


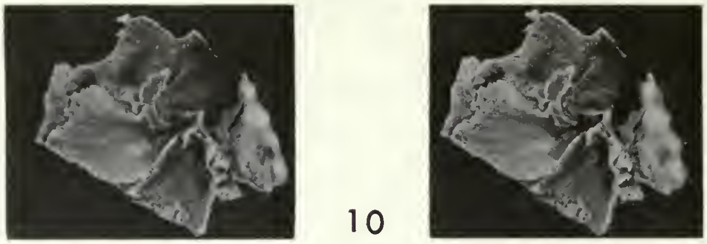
Fig. 9 Drawings from silicified specimens of *Tretorhynchia trilatera*. Fig. 9a, ventral valve umbo showing the crytomatodont teeth and open delthyrium (see also Fig. 20). Fig. 9b, c, the cardinalia within a dorsal valve looking dorsally and posterodorsally. isr = inner socket ridge; ihp = inner hinge plate; cb = crural base, and ms = median septum (see also Fig. 12a–c).

The dorsal cardinalia are essentially as previously illustrated (Brunton 1971: 105, text-fig. 16) but the following differences should be noted. The inner socket ridges follow the valve edge closely, overhanging the sockets, and the inner hinge plates recurve posteriorly, at the point of their fusion with the median septum, more than was indicated (Figs 11, 12). The crura are blade-like, in the vertical plane, at their junction with the hinge plates and their development can be traced posteriorly as ridges (crural bases) on the dorsal surface of the hinge plates (Brunton 1971: 101, text-figs 6–8 and Fig. 10 herein).

A deep pit between the posterior ends of the inner sockets ridges is interpreted as the site of attachment of the diductor muscles. During ontogeny the inner hinge plates grew to about 0·8 mm long, by which time the shell was 5–8 mm long, and thereafter only the articulation structures, crura and median septum grew anteriorly. Thus in juvenile shells the sockets and teeth are situated lateral to the anterior edges of the hinge plates, while in adult shells the teeth are positioned well to the front of the hinge plates and bases of the crura. This anterior migration of the points of articulation enhanced the efficiency of the lever system used by the diductor muscles in opening the shell. In this way the diductor muscles may have retained efficiency as the shell increased in size without having to increase their muscle fibre content to any great extent.

The crura extend to a length of at least 1·5 mm from the dorsal umbo, a little more than suggested in 1971, and they curve ventrally in an arc. Distally, the crura are wide and somewhat concave anterodorsally. The median dorsal septum is about 2 mm long in valves about 9 mm long and remains at this length during any further growth of the valve.

ONTOGENY. Twenty-three juvenile shells ranging in length from 1·5 mm to 4·0 mm were measured. Incomplete valves indicate that specimens of about 10·0 mm long were present in the asssemblage. The plotted measurements of 23 specimens extend the plots of length, width and thickness of the non-silicified material (Brunton 1971: 103–4, text-figs 13–15) towards zero. Of 14 dorsal valves on which the ribs could be counted with confidence, 2, 6, 3 and 3 specimens had 15, 16, 17 and 18 ribs. On the non-silicified material previously studied the mean value was 18 dorsal ribs, with a maximum of 24 on 3 specimens out of 43. The ribs over the dorsal and ventral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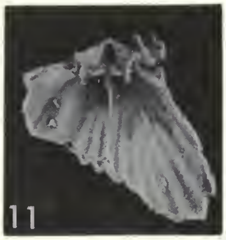
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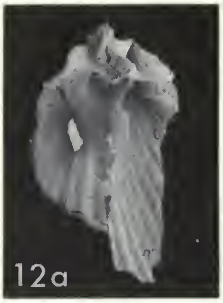
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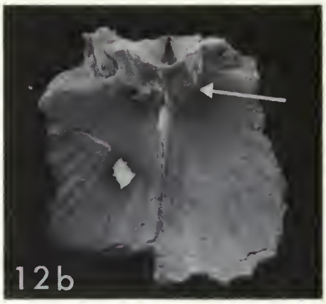
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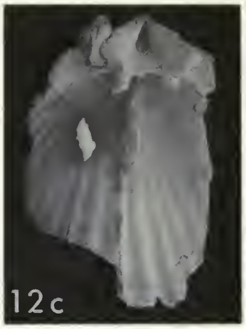
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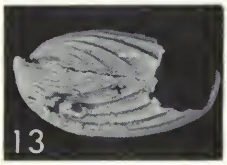
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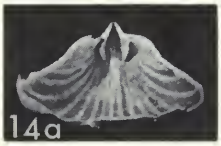
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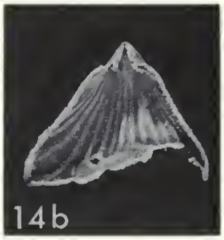
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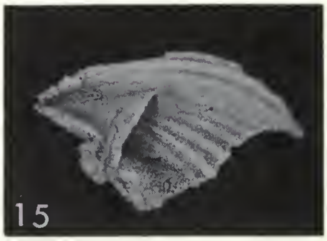
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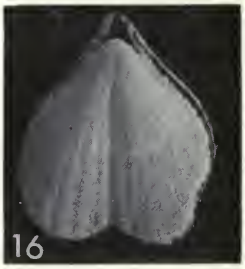
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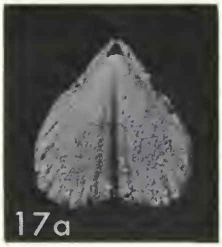
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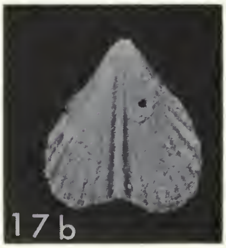
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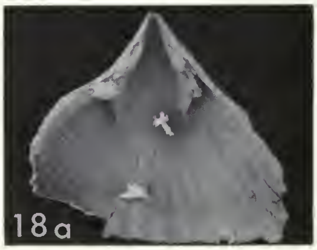
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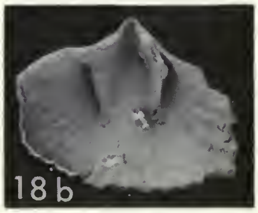
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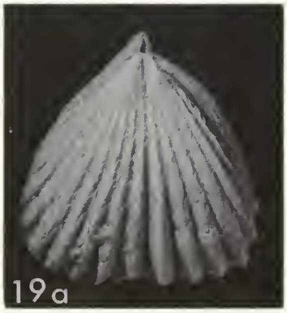
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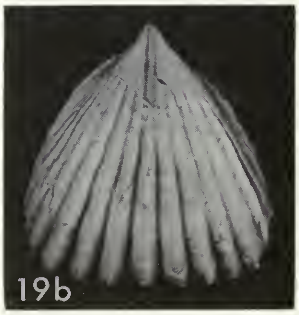
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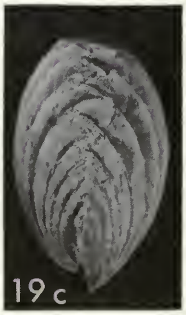
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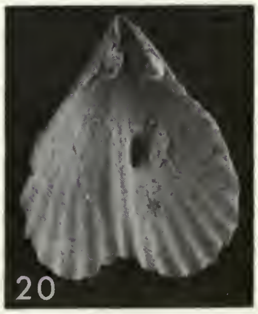
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surfaces of *T. trilatera* are normally true costae, the branching or addition on ribs beyond the first mm being extremely rare (Fig. 19). Laterally, on the sides of the umbones, two or three pairs of ribs may have developed while the shells were between 4 mm long and adulthood. On three well-preserved specimens 4 mm long the full 18 costae can be counted. Thus the fewer ribs on the silicified specimens correlates with their smaller size and juvenile condition.

Discussion. As with Recent rhynchonellides, the adult dorsal umbo is tucked into the delthyrial opening of the ventral valve so that in the act of opening the pedicle aperture was not obstructed. The delthyrium (pedicle aperture) remained open and presumably functional throughout ontogeny (Figs 17a, 19a). Very rarely the slight development of deltidial plates confined the aperture to some extent. No signs of abrasion have been recognized at the umbones, such as would be expected had the shells been attached to a hard substrate in a high-energy environment. The restraints of the articulatory processes probably allowed a gape of no more than 25° in living *T. trilatera* and the specimens are thought to have lived on a soft substrate attached to small shelly fragments of bryozoans or brachiopods. Few bored shells have been observed (but see Figs 17b, 20) and the only ones showing any signs of infestation are fragments of old shells which may, therefore, have been invaded after the death of the brachiopod.

The Fermanagh occurrence of *T. trilatera*, from rocks of low D Zone age, does not extend the mid to upper Viséan stratigraphic range given in 1971, but slightly extends to the north-west the known geographical range. In addition, the species has been recorded from Breedon, Leicestershire, by Monteleone (1973).

Superfamily **STENOSCISMATACEA** Oehlert 1887 (1883)

The taxonomic position of the Stenoscismatacea is not agreed universally. Rudwick (1970) derived the superfamily from the Pentameracea, but the more common view is that adopted by Grant (1965) in placing stenoscismataceans within the Rhynchonellida. Preliminary observations on the shell structure of *Coledium* indicate a standard sequence of a thin primary shell layer followed by a thicker, coarsely fibrous secondary layer. This is as in rhynchonellaceans, whilst the shell structure of some pentameraceans is complicated by the addition of a tertiary layer, more akin to the situation seen in many spiriferids.

Members of the superfamily have only rarely been recorded from Carboniferous rocks in Britain. In older literature species now assigned here might appear under the Camarophoriacea (e.g. Sibly 1906, *Camarophoria isorhyncha* (M'Coy) or *C. globulina* var. *rhomboidea* (Phillips) in Davidson, 1861). Stenoscismatacea species are recorded infrequently in faunal lists under

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Figs 10–20 *Tretorhynchia trilatera* (de Koninck). Fig. 10, stereoscopic pair of photographs showing the posterior internal morphology, with the ventral valve uppermost. The crus on the left is almost complete; that on the right is broken and exposes the socket and tooth. BB63666, ×5. Fig. 11, incomplete dorsal valve interior, with a tooth still in place on the right side. BB63668, ×6. Fig. 12a–c, scanning electron micrographs (S.E.M.) of an incomplete dorsal valve interior (plus a tooth in the left socket) showing the median septum and cardinalia, including the thickened crural bases below the hinge plates (arrowed). BD174, ×6·7, 8·5 and 7·5 respectively. Fig. 13, incomplete young shell viewed laterally. BB63669, ×3. Fig. 14a, b, incomplete young ventral valve viewed posteriorly to show the dental plates, and ventrally. BB63670, ×3. Fig. 15, incomplete ventral valve viewed laterally to show the median face of the dental plate, on which growth lines are distinguishable. BB63665, ×8. Fig. 16, S.E.M. dorsal view of a juvenile specimen showing the early dorsal folding and anterior margin. BD177, ×11. Fig. 17a, b, dorsal and ventral valves of a juvenile specimen showing the juvenile outline and accentuated ventral median rib (cf. Fig. 19b). BB63664, ×10. Fig. 18a, b, S.E.M. of incomplete ventral valve showing the cyrtomatodont teeth and dental plates. BD175, ×5·6 and 4·7 respectively. Fig. 19a–c, adult specimen from Wetton, Staffordshire, viewed dorsally, ventrally and laterally. BB58455, ×3. Fig. 20, S.E.M. of young ventral valve interior showing the hook-like teeth; traces of the endopunctation can be seen on the internal surface anteriorly. BD178, ×8·7.

non-stenoscismatacean genera, and were first fully described in British literature within the modern concepts of the group by Brunton & Champion (1974). Martinez-Chacon (1977) has described stenoscismatacean brachiopods from the Upper Carboniferous of Spain.

Family **STENOSCISMATIDAE** Oehlert 1887 (1883)

Genus ***COLEDIUM*** Grant 1965

Type species. *C. erugatum* Grant 1965, by original designation; from the Moorefield Formation, Meramec, Mississippian of Oklahoma, U.S.A.

Grant's (1965) important monograph on the superfamily, upon which the *Treatise* (Williams *et al.* 1965) section is based, included the descriptions of *Coledium globulinum* (Phillips), a Permian species, and figured specimens assigned to *Coledium rhomboideum* (Phillips). The specific name *pleurodon* Phillips should not be included within *Coledium*, as it forms the type species of a true rhynchonellacean genus, *Pleuropugnoides*. *C. globulinum* (Phillips) was named only in a plate explanation (Phillips 1834) and the species was not described until Davidson's monograph (1858). Phillips' plate explanation indicates that he intended the species for a Permian fossil, although the name appears neither in his list of Permian (1834: 617) nor Carboniferous (1834: 1605) fossils. I have not been able to recognize any specimens of this species known to have been seen by Phillips. Phillips' specimens of *C. seminulum* (Phillips, 1836) are in the British Museum (Natural History), London, and came from Viséan rocks of Bolland (Fig. 21). Both Davidson and Grant considered these species synonymous and from external characteristics this seems possible, despite the resulting long time range. However, there is a difference in the ribbing and

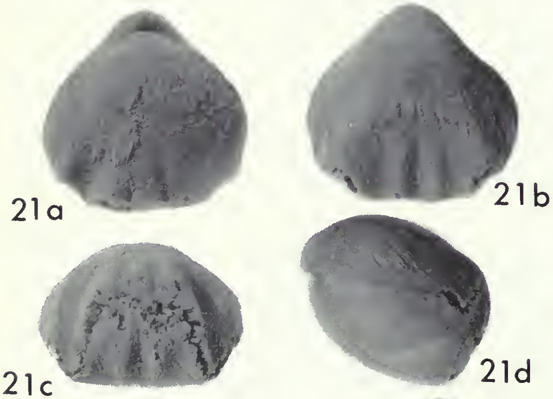


Fig. 21 *Coledium seminulum* (Phillips). Lectotype, selected Brunton & Champion (1974), viewed dorsally, ventrally, anteriorly and laterally. Viséan of Bolland, Yorkshire. B355, ×6.

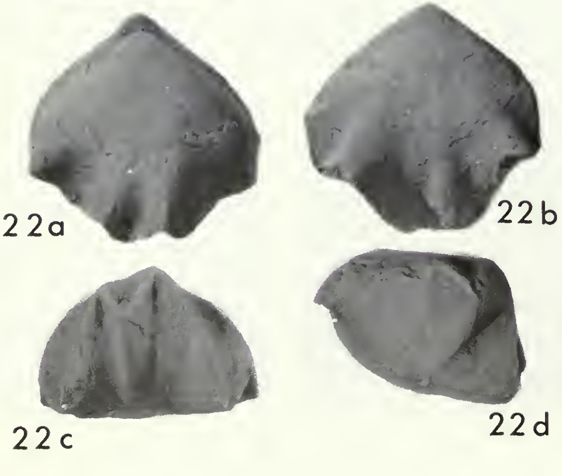


Fig. 22 *Coledium rhomboideum* (Phillips). **Lectotype** herein selected, viewed dorsally, ventrally, anteriorly and laterally. Viséan of Bolland, Yorkshire. B354, ×3.

folding: out of the 9 specimens of *seminula*, seen by Phillips, 8 have 3 ribs on the dorsal fold whilst out of 17 Permian specimens from Co. Durham assigned to *globulina* 16 have a smooth to 2-ribbed fold and only one specimen closely resembles *seminula* in this feature. All specimens are of the same order of size (5–7 mm long). Comparative studies of interiors are required before relating these species, but it seems likely that there are sufficient morphological differences within this group of *Coledium* to warrant specific separation.

Davidson (1861: 115) synonymized Phillips' three species *globulina* 1834, *seminula* 1836 and *rhomboidea* 1836, believing the first two names to represent the young of *rhomboidea*. At the size attained by most specimens of *seminula* (about 5 mm long), specimens assigned to *rhomboidea* (Fig. 22) do not show ribbing deflections of the anterior commissure, although it is already unisulcate. Furthermore the relative thickness of *seminula* is greater whilst the relative width of *rhomboidea* is slightly greater. *Coledium rhomboideum* (Phillips) is closely comparable externally to *C. explanatum* (McChesney) from the late Mississippian of the U.S.A. They differ internally in that *C. rhomboideum* has a spondylium supported by a high median septum, while that of *C. explanatum* is sessile and raised on a low median septum anteriorly (Weller 1914: 124). Martinez-Chacon (1977) has pointed out that should *C. globulinum* (Phillips) prove not to have an intercamarophorial plate, the species should be assigned to *Cyrolexis*. In Britain *C. rhomboideum* is known from the D Zone 'reef' limestones of Staffordshire, Derbyshire and the type area, Bolland.

Coledium seminulum (Phillips)
Figs 21, 23–29

v* 1836 *Terebratula seminula* Phillips: 222; pl. 12, figs 21–23.
1861 *Camarophoria globulina* (Phillips) Davidson: 115; pl. 24, figs 13–16.
1974 *Coledium seminulum* (Phillips); Brunton & Champion: 824; pl. 109, figs 1–9.

DIAGNOSIS. Small globose *Coledium*, reaching about 8 mm in length, with three ribs on dorsal fold. Spondylium elevated on low median ridge.

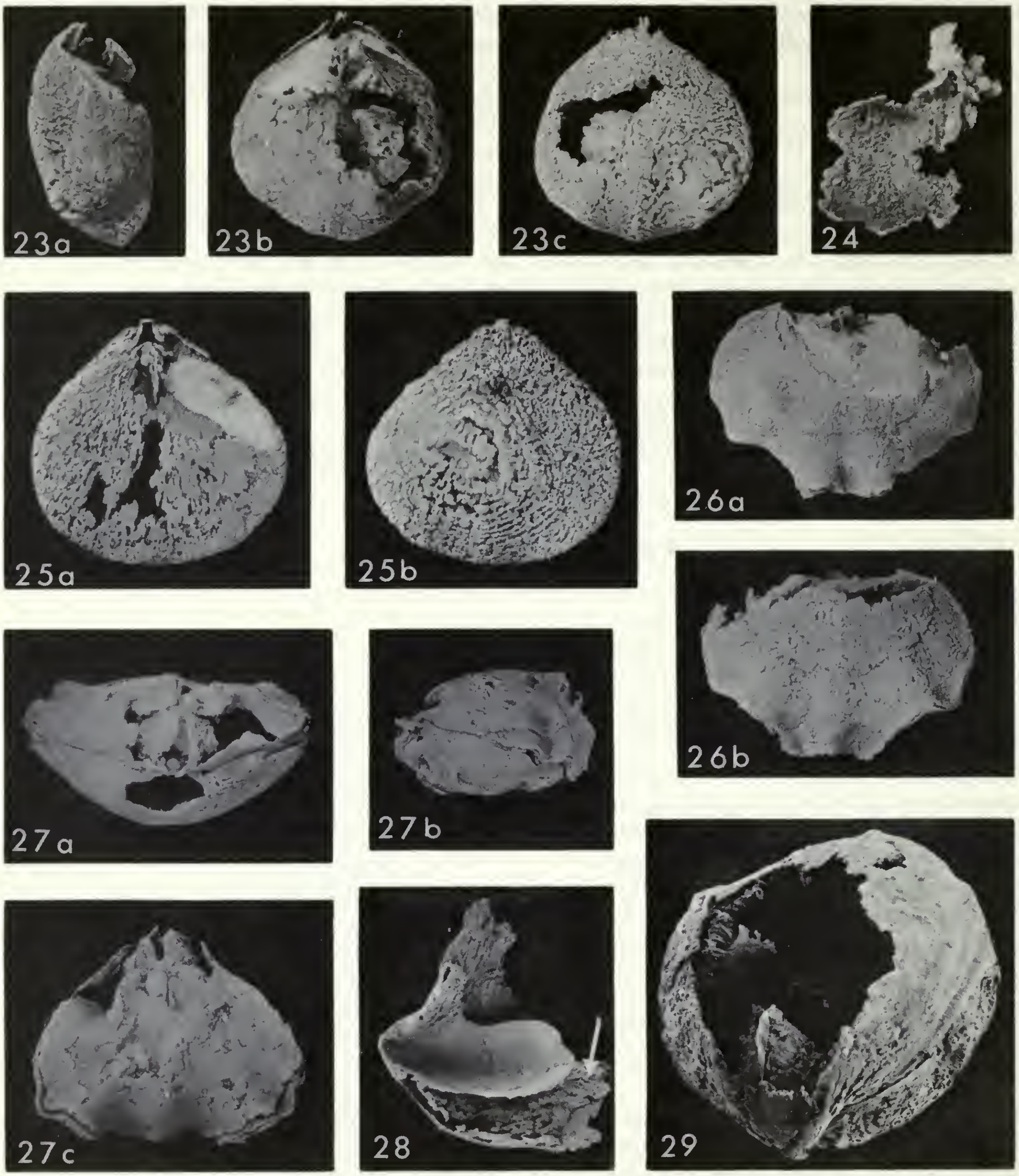
DESCRIPTION. Small globose *Coledium* with subcircular outline. Uniplicate anterior commissure normally modified by three ribs on dorsal fold. Ventral umbo pointed, with narrowly triangular delthyrium directed dorsally. Dental plates fusing to floor of valve, extending anteriorly as slightly expanded spondylium elevated on low median ridge. Short imperforate hinge plate supporting blade-like crura. Camarophorium narrow, curving anteroventrally and supported by high median septum; intercamarophorial plate low and not connecting to hinge plate.

LECTOTYPE. Selected by Brunton & Champion (1974), *T. seminula* Phillips, 1836: pl. 12, fig. 23, from Bolland, Yorkshire. Gilbertson Collection, BM(NH), B355. Figured here as Figs 21a–d.

MATERIAL. Lectotype plus eight other specimens in the Gilbertson Collection from Bolland. Silicified material from the Sillees river locality yields fifteen specimens, many of which are incomplete.

DISCUSSION. Davidson (1861) thought that specimens called *seminula* by Phillips were only the young of Phillips' species *rhomboidea* (Fig. 22). The evidence afforded by the silicified specimens and sections of specimens attributed to *rhomboidea* shows that the internal structures are distinctive and supports the validity of there having been two species. As mentioned above, the spondylium of *C. rhomboideum* is supported on a high median septum from its origin in the beak. The spondylium of *C. seminulum* is sessile, being developed posteriorly from the fusion of dental plates with the valve floor, and only anteriorly it is raised above the valve floor on a low median septum (Figs 28, 29).

The species is insufficiently represented in the Fermanagh faunas to allow conclusive ontogenetic study, but Brunton & Champion (1974) described the growth of the species from specimens collected about one mile west of Wetton village, north Staffordshire. Up to a length of about 3·5 mm the shells grew with a regular, smooth, gently biconvex profile. Beyond this length the plication of the commissure and median ribs developed. Opposed growth at the valve



Figs 23–29 *Coledium seminulum* (Phillips). Fig. 23a–c, lateral, dorsal and ventral views of young shell showing the start of folding at its anterior margin. BB63672, ×5. Fig. 24, incomplete young ventral valve with spondylium. BB63675, ×7. Fig. 25a, b, juvenile shell, before the onset of anterior folding, in dorsal and ventral aspects; in the former, the base of the spondylium and the median septum can be seen. BB63673, ×7. Fig. 26a, b, anterior part of adult shell showing the folding and marginal ribs in dorsal and ventral aspect. From Carrick Lough. BB63620, ×4. Fig. 27a–c, incomplete adult shell in posterior, lateral and ventral views. BB63671, ×4. Fig. 28, internal posterior region of a ventral valve with its spondylium, supported anteriorly on the median septum (arrowed). BD191, S.E.M. ×15·5. Fig. 29, posteroventral regions of young specimen, showing the spondylium. BD1169 (specimen destroyed), S.E.M. ×20.

margins increased the relative thickness of the shell (depth of the body cavity), and the camarophorium grew ventrally. Only in the largest shells, more than about 8 mm long, did lateral ribbing develop.

Being a small species it has probably been overlooked in several localities. Other than the type area, Bolland, and the Fermanagh occurrences I know of the species in north Staffordshire, and in large numbers from the Poyllvaaish Limestone near Castletown, Isle of Man, also in Asbian, Viséan rocks.

Order **SPIRIFERIDA** Waagen 1883

Superfamily **RETZIACEA** Waagen 1883

Family **RETZIIDAE** Waagen 1883

Genus ***HUSTEDIA*** Hall & Clarke 1893

TYPE SPECIES. *Terebratula mormoni* Marcou 1858: 51, from 'Mountain Limestone' strata near Salt Lake City, Utah, U.S.A. Work by Sutherland & Harlow (1973) indicates a Pennsylvanian, Desmoinsian, age for this species.

DESCRIPTION. Broadly elliptical to circular or broadly ovate in outline, subequal biconvex in profile. Equicostate shells commonly lacking fold or sulcus. Deltidial plates conjunct, foramen permesothyridid. Dental plates lacking; with or without pedicle collar. Cardinalia typically with posteriorly recurved median prong-like ligulate process. Jugal lamellae rising anteroventrally and spinose stem projecting posteriorly from saddle.

DISCUSSION. The type species of the genus was well described by Hall & Clarke who figured the cardinalia and part of the spiralia. These authors suggested that the European species *Terebratula radialis* Phillips, *Retzia carbonaria* Davidson and *T. ulothrix* de Koninck should be included in *Hustedia*. The acceptance of *H. ulothrix* within the genus necessitates revision of the generic diagnosis given in the *Treatise* (Williams *et al.* 1965: H652).

Several different species names have been used for shells belonging to *Hustedia* from British and Belgian Lower Carboniferous strata. Davidson, who is well known for his grouping of fossil species, in describing *H. radialis* (1863: 218) wrote that this 'shell appears to have varied considerably in shape, as well as in the number and size of its ribs, so much so that many of its variations when viewed individually might lead us to doubt their being simple modifications of Phillips' type'. He went on to describe how the extreme forms could be linked by intermediate forms. He considered them all to be of the same species and said that he illustrated 'the most marked variations' in his plates. In addition to *H. radialis* Davidson recognized *H. ulothrix* and described for the first time the species *carbonaria**, assigned either to *Retzia* or *Rhynchospirina*. Davidson sent drawings of his species to Hall who later included it in *Hustedia*. By contrast de Koninck (1887) figured six species of *Retzia* which would now be placed in *Hustedia*. All save for *radialis*, which he synonymized with *mormoni*, were his own species; *ulothrix, buchiana, multiplicata* (*multicostata* is the name used on the plate explanation) and *intermedia*. He did not record *carbonaria*, although Davidson had sent him drawings for comment. *H. ulothrix* and *H. buchiana* are distinct from *H. radialis*, to which the other de Koninck 'species' are closely related, or subspecific variants.

Study of *Hustedia* specimens in the BM(NH) collections shows that the common range in the number of costae on dorsal valves of *H. ulothrix* is 7 or 9, on *H. mormoni* 13 to 15 and on *H. radialis* 18 to 21. (Sutherland & Harlow, 1973, give an average of 14·4 ribs, range 12–17, on 26 specimens of *H. mormoni* from the Desmoinsian of New Mexico.) We have little knowledge of the interiors of *Hustedia* species at present described from Lower Carboniferous rocks. The variation demonstrable within a fossil assemblage, such as that from Fermanagh, supports Davidson's (1863) contention that the various forms similar to *H. radialis* should be grouped under that species name. In the future if we have large samples, including the variety of forms at present named, it may be possible to provide distinctive characteristics for several species.

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*The original specimen of *Retzia carbonaria* Davidson (1863: 219; pl. 51, fig 3) is in the IGS collections at Leeds, No. 86028; a replica is in the BM(NH) collection, BB58683. This specimen is partially silicified but can be seen to have been endopunctate from the areas of unaltered shell. Davidson's figures have been restored to some extent but are a close likeness to the specimen, which is 19·6 mm long, 15·8 mm wide and 11·3 mm thick; the dorsal valve has about 21 costae and no costellae are visible. It seems possible that the specimen is an unusually large example of *Hustedia radialis* (Phillips).

Hustedia radialis (Phillips)

Figs 30–38

v* 1836 *Terebratula radialis* Phillips: 223; pl. 12, figs 40, 41.
1861 *Retzia radialis* (Phillips) Davidson: 87; pl. 17, figs 19–21.
1863 *Retzia radialis* (Phillips); Davidson: 218; pl. 51, figs 4–9.
1887 *Retzia radialis* (Phillips); de Koninck: 94; pl. 22, figs 16–19.
(?)1887 *Retzia multiplicata* de Koninck: 95; pl. 22, figs 20–24.
v. 1974 *Hustedia* cf. *radialis* (Phillips); Brunton & Champion: 825; pl. 109, figs 10–18.

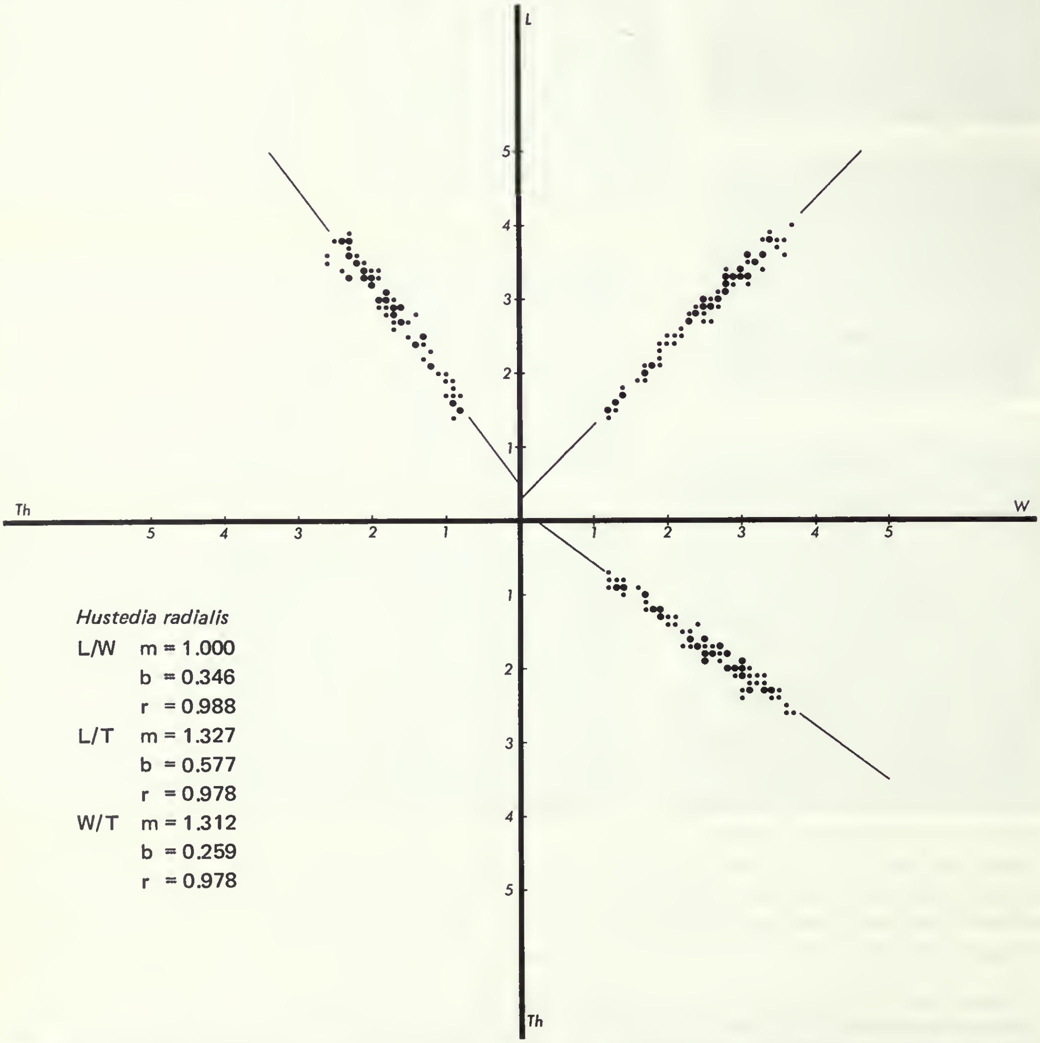
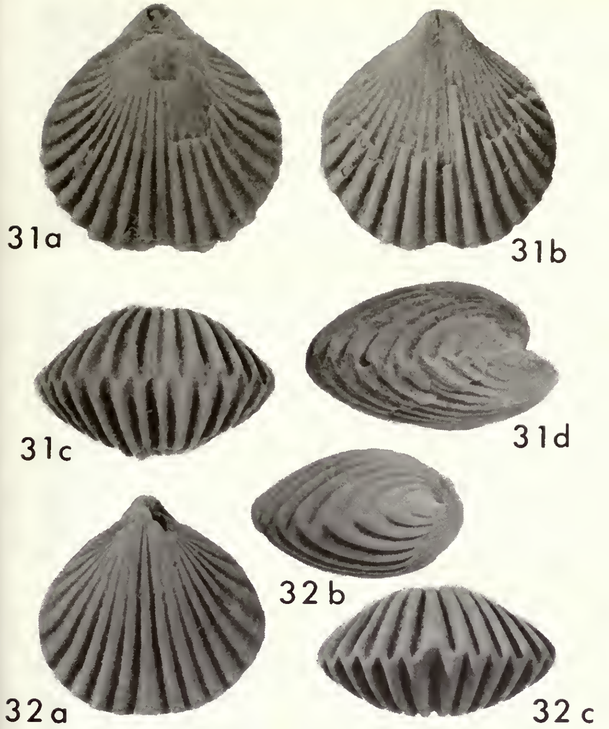


Fig. 30 *Hustedia radialis* (Phillips). Length, width and thickness plots of 90 specimens from Co. Fermanagh. m = slope of the regression line; b = intersection point of m with an axis; r = coefficient of correlation between two attributes.



Figs 31–32 *Hustedia radialis* (Phillips), Gilbertson Collection, Bolland, Yorkshire. Fig. 31a–d, dorsal, ventral, anterior and lateral view of a small paralectotype. BB65230, ×6. Fig. 32a–c, dorsal, lateral and anterior views of **lectotype** (herein selected). B328, ×3.

Diagnosis. Subcircular to broadly ovate in outline, biconvex in profile. Costate, commonly 19 or 20 costae on each valve (range 17–23), short pedicle collar and cardinalia as for genus, endopunctation coarse, about 25 per mm^2 on lectotype.

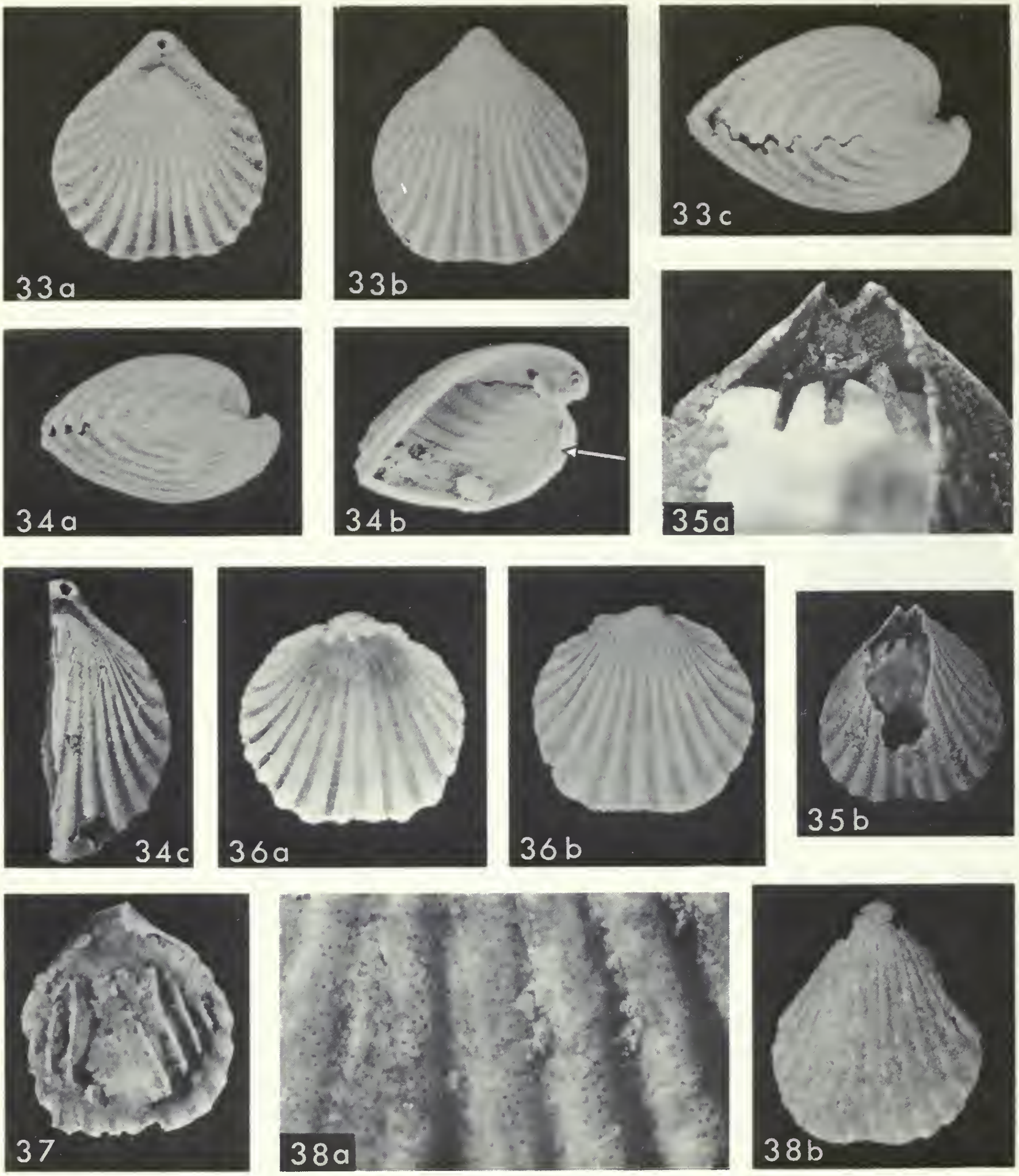
Lectotype. Here selected, from the Gilbertson Collection in the BM(NH), B328; specimen figured by Phillips, pl. 12, figs 40, ?41, from Bolland, Yorkshire (Fig. 32a–c).

Material. In the Gilbertson Collection there are six specimens from Bolland labelled '*T. radialis* Phillips'. Two are relatively large, the lectotype (Fig. 32) 9·6 mm long, and a second less well-preserved specimen 9·7 mm long. The other four are only about 5·0 mm long (e.g. BB65230, Fig. 31) and are thus much more like the Fermanagh silicified specimens. That the two illustrated specimens belong to the same species is debatable; at present I believe there is insufficient evidence to separate them and accordingly name the Fermanagh specimens *H. radialis*. The lectotype was chosen because it was the specimen figured by Phillips. If in the future the small specimens prove to be distinct they will have to be renamed and *radialis* would then be restricted to the more broadly ovate specimens, which perhaps are characterized by fewer costae, a maximum of 18 dorsal as compared to 23 on the small specimens.

The species is one of the commonest from the etched faunas, there being several hundreds of specimens from the two principal localities at the Sillees river and Carrick Lough.

Description. The Fermanagh silicified specimens are small, ranging from about 1·5 mm to about 4.0 mm long (Fig. 30). The larger, perfectly preserved specimens show 21 dorsal costae. This compares with 18 on the lectotype and 19 or 20 on the second large Gilbertson specimen, and 20 to 24 costae on the four small specimens.

In the ventral valve the deltidial plates are medially fused with no clear line of junction, thus forming a symphytium. The pedicle collar is small and restricted to a thickened rim around the inside of the pedicle aperture (Fig. 34b). Signs of the muscle scars have not been observed in ventral valves. In dorsal valves there is a slight median ridge extending anteriorly from below the hinge plate for about one mm, within the umbonal region. This ridge separated the adductor



Figs 33–38 *Hustedia radialis* (Phillips), from Co. Fermanagh. Fig. 33a–c, adult specimen in dorsal, ventral and lateral views. BB63410, ×10. Fig. 34a, b, half a complete shell viewed laterally, externally and internally, showing the small pedicle collar, part of the cardinal process and the low dorsal median ridge (arrowed). BB63408, ×8. Fig. 34c, same specimen viewed dorsally. BB63408, ×10. Fig. 35a, b, incomplete shell with part of the ventral valve missing, showing the ventral aspect of the three-pronged cardinal process as it curves towards the inner surface of the deltidial plates. BB63412, ×25 and ×8 respectively. Fig. 36a, b, internal and external views of adult dorsal valve, BB63409, ×10. Fig. 37, inside of a ventral valve to which part of the spiralium is stuck by siliceous deposits. BB63413, ×10. Fig. 38a, b, anterior of a ventral valve, without ammonium chloride spray, to show the endopunctation replicated in the silicified shell. BB63497, ×40 and ×10 respectively.

muscle areas and was present from an early stage of ontogeny. In young dorsal valves about 2·0 mm long the cardinalia would appear to have lacked the median ligulate process. This may be the result of preservation failure in the smallest valves, but by a length of about 2·5 mm there are signs of this process having developed (Fig. 35).

H. radialis appears to be devoid of growth lines, rendering it impossible to check the ontogeny of an individual against the results obtained from the variously-sized specimens in the sample as a whole. One cannot tell if the wider, more circular outline of the large Gilbertson specimens results simply from their larger size. From the available data on external dimensions, growth would seem to have been isometric except in the earliest stages (to about 1·5mm long) when thickness increased more slowly than later in life.

DISCUSSION. Judged by specimens of *H. mormoni* from the Pennsylvanian of Texas and Kansas in the BM(NH) collections, and from published information by Hall & Clarke (1893) and Sutherland & Harlow (1973), this species differs from the type of *H. radialis* by being more elongate and in having only 13 to 15 dorsal costae. *H. texana* Girty 1926, as described and refigured by Carter (1967), from low Mississippian (high Tournaisian) strata of North America is very similar to *H. radialis*. From Carter's measurements (1967: 322) *H. texana* is about two-thirds as thick as specimens of the same length from Fermanagh, but of very similar relative thickness to the four small specimens in the Gilbertson Collection. Carter writes that he found 'no pedicle collar in sectioned specimens' (1967: 319). Unfortunately his figures do not include the ventral umbo, but if *H. texana* should prove to have a small pedicle collar it seems likely that it would be conspecific with *H. radialis*. Roberts (1971) has described *H. paula* from the Utting Calcarenite ($\equiv D_1$) of north-western Australia, and this species is similar to *H. radialis*. His specimens are small (up to 6·5 mm long) and of the same general shape, but perhaps differ in having only 17 dorsal valve costae (within the range of Fermanagh specimens). The dorsal valve interiors of *H. paula* Roberts are more strongly featured than those of the Fermanagh specimens; the muscle scars, median ridge and vascular ridges all show clearly in his figured specimen (1971: pl. 37, figs 14, 15).

Silicified specimens from Viséan strata in north Staffordshire, assigned to *H.* cf. *radialis* by Brunton & Champion (1974), are very similar to the Fermanagh specimens in all respects except that they have fewer ribs and the thickness of the shell is slightly less in the Staffordshire material.

Probably because of their small size *Hustedia* specimens are uncommonly recorded in Britain, except from areas in which it has been possible to develop by acid solution of the rock. So far such acid-developed faunas have contained no large specimens like the lectotype. This may be the result of sampling areas which are marginal to the main habitat of this species. Both the Fermanagh and north Staffordshire silicified faunas come from fine-grained, rather argillaceous limestones unlike the 'clean' limestone 'reefal' facies from which the lectotype probably came.

Hustedia ulothrix (de Koninck)
Figs 39–43

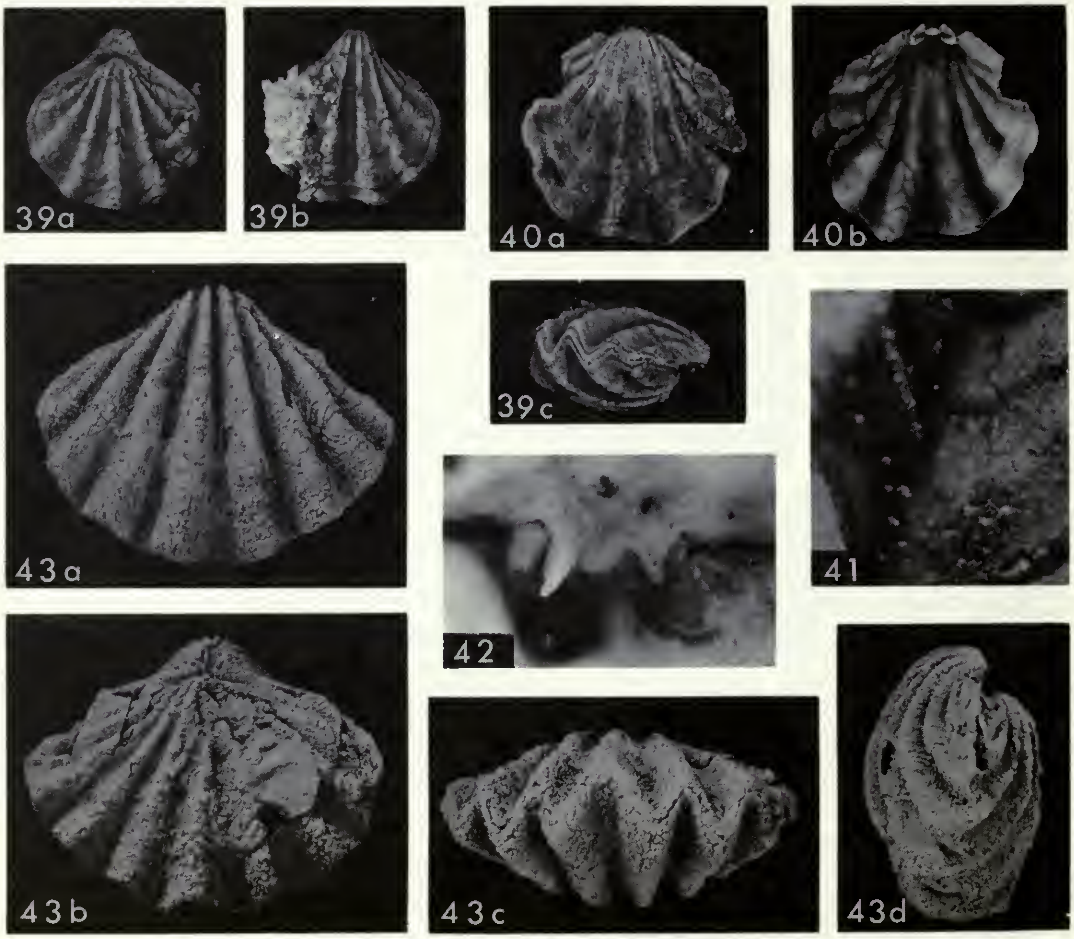
1843 *Terebratula ulotrix* de Koninck: pl. 19, figs 5 (on p. 292 named as *crispata*; this name recognized as preoccupied and species renamed on plate explanation).
1861 *Retzia ulotrix* (de Koninck) (*sic*) Davidson: 88; pl. 18, figs 14, 15.
1863 *Retzia ulotrix* (de Koninck) (*sic*); Davidson: appendix pl. 54, fig. 45.
v* 1887 *Retzia ulothrix* (de Koninck); de Koninck: 92; pl. 22, figs 1–4.
1887 ?*Retzia davidsoni* (de Koninck) de Koninck: 92; pl. 22, fig. 10.

DIAGNOSIS. Coarsely ribbed (7 or 9 on dorsal valves) *Hustedia* with dorsal median rib. Ventral valve with prominent umbo, long interarea and ? lacking pedicle collar. Cardinal process lacking median ligulate process.

LECTOTYPE. The specimen figured by de Koninck (1843: pl. 19, figs 5a–c) as *Terebratula ulotrix*, and again (1887: pl. 22, figs 1–4) as *Retzia ulothrix*, is apparently (de Koninck 1843: 292) one of two originally examined by him. It is here selected lectotype (Fig. 43a–d). It is in the collections of the Institut Royal des Sciences Naturelles de Belgique, Brussels; cast in the BM(NH), no. BB61404. The four figures of 1887 are different superficially from those of 1843, but on close inspection, along with the chosen specimen, it seems probable that both sets of drawings were made from the same original. I believe, therefore, that the chosen specimen is one of the two originally mentioned by de Koninck.

NAME. The trivial name was first printed as *ulotrix* (de Koninck 1843), as a substitute for *crispata*, in the plate explanation. It seems clear that this was a printers' error, for not only were all subsequent de Koninck references spelt *ulothrix* but labels written by de Koninck use this spelling.

MATERIAL. In the Fermanagh faunas this species is rare. The Sillees river locality has yielded only four complete shells plus seven more or less complete valves (4 dorsal, 3 ventral). The largest specimen (7·5 mm long, 7·2 mm wide, 4·0 mm thick) is small by comparison with those in museum collections, a feature common to most species recovered from these limestones. The



Figs 39–43 *Hustedia ulothrix* (de Koninck). Fig. 39a–c, dorsal, ventral and lateral views of young specimen from the Carrick Lough locality. BB63425, ×3. Fig. 40a, b, dorsal valve, exterior and interior, showing the inner socket ridges and relatively simple cardinal process. BB63417, ×5. Fig. 41, part of ventral valve exterior anteromedially, showing the microspinose ornamentation. BB63416, ×20. Fig. 42, anteroventral aspect of cardinalia showing teeth, the strong inner socket ridges and lack of a median process. BB63415, ×14. Fig. 43a–d, **lectotype** (herein selected), from the de Koninck collection in Brussels, viewed ventrally, dorsally, anteriorly and laterally. ×3.

smallest shell is only 3·4 mm long, 2·8 mm wide and 1·6 mm thick. This and other incomplete valves indicate that the sample contains a wide range of sizes of specimen and it seems likely that it represents an assemblage preserved close to the site of the original living population.

Discussion. Two internal morphological features differ from those normal for the genus: the lack of a pedicle collar and the lack of a median ligulate process on the cardinalia (Figs 40b, 42). These features were figured and described in the original description of *Hustedia* by Hall & Clarke (1893) and are repeated in the brachiopod *Treatise* (William *et al.* 1965). The question arises, therefore, whether to widen the generic description to include this species or to suggest a new generic name. The former procedure has been adopted as the gross form of other morphological features is comparable in *H. ulothrix, H. radialis* and (from illustrations and specimens in museum collections) *H. mormoni.*

The species is rare and seems only to have been recorded in the British Isles from Bolland, West Yorkshire; Wetton and Alstonefield, Staffordshire (Davidson 1861, 1863); the Settle district of Yorkshire (Garwood & Goodyear 1924); Black Rock, ? Co. Cork, Ireland (Davidson Collection); and from silicified material in the Manifold valley, near Wetton, Staffordshire (Brunton & Champion 1974).

Superfamily **ATHYRIDACEA** Davidson 1881

Family **ATHYRIDIDAE** Davidson 1881

Subfamily **ATHYRIDINAE** Davidson 1881

In the past this family and subfamily have been assigned to M'Coy, 1844 (e.g. Williams *et al.* 1965). However, Alvarez, Brime & Brunton (1980) point out that M'Coy's use of the name 'Athyridae' does not comply with the rules of the International Code of Zoological Nomenclature (Stoll *et al.* 1964), in that it did not, in 1844, contain the generic name *Athyris*. Not until 1881 was *Athyris* placed in the 'Athyridae' by Davidson. Type specimens of several Upper Palaeozoic athyrid species have been selected and described briefly (Brunton 1980), including the type species of two genera in the Fermanagh fauna, *Actinoconchus* and *Cleiothyridina*.

Genus *ACTINOCONCHUS* M'Coy 1844

Type species. *Actinoconchus paradoxus* M'Coy (1844: 150; pl. 21, figs 6a, b). The only species described by M'Coy in his new genus. See Brunton (1980: 221) for details of the species.

Diagnosis. Athyridinae with long, delicate, non-spinose flanges of shell from rugae or strong growth-lines on both valves.

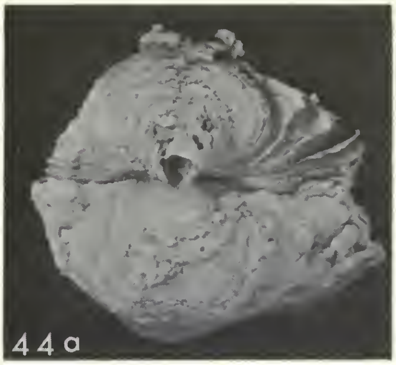
Actinoconchus lamellosus (Léveillé)

Figs 44–51

1835 *Spirifer lamellosus* Léveillé: 39; pl. 2, figs 21–23.
v* 1836 *Spirifera squamosa* Phillips: 220; pl. 10, fig. 21.
v. 1859 *Athyris lamellosa* (Léveillé) Davidson: 79; pl. 16, figs 1, 1a, b.
v. 1863 *Athyris lamellosa* (Léveillé); Davidson: pl. 51, fig. 14.
1887 *Athyris lamellosa* (Léveillé); de Koninck: pl. 21, figs 1–3, ?4, 5, (?6–8), 11, 12.
1965 *Athyris lamellosa* (Léveillé); Boucot, Johnson & Staton *in* Williams *et al.*: fig. 537, 4b, c, d.

Diagnosis. *Actinoconchus* with depressed obovate outline, ventral sulcus and low dorsal fold with or without shallow sulcus. Shell flanges long and radially corrugated, extending from rugae of both valves.

Type specimens. Léveillé's types appear to be lost (Gaetani 1968: 711). M'Coy (1844: 148) synonymized *S. squamosa* Phillips 1836 (Lectotype B309 in the Gilbertson Collection of the BM(NH), London) with *S. lamellosus* Léveillé 1835. This has been accepted by most subsequent authors. Specimens from Belgium named by de Koninck as *Athyris lamellosa* (Léveillé), now in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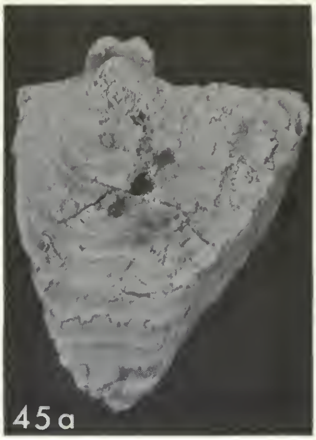
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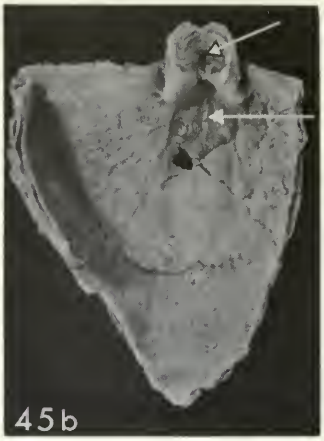
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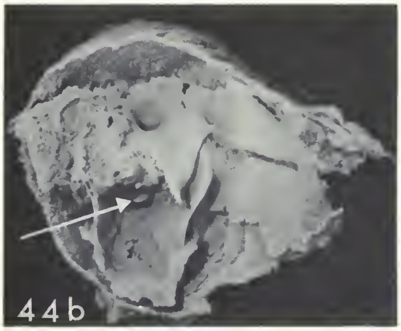
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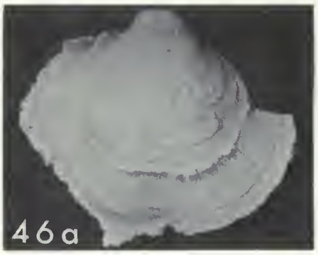
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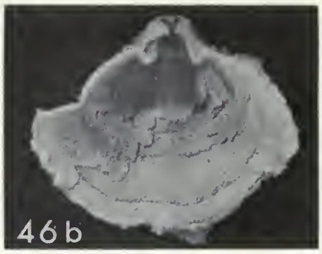
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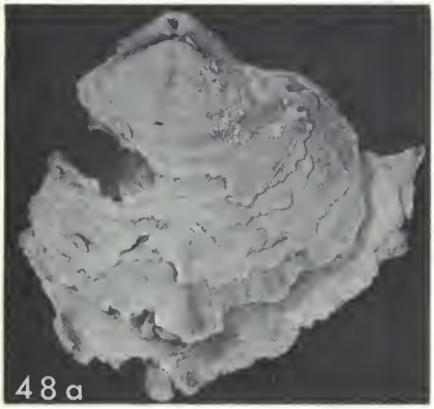
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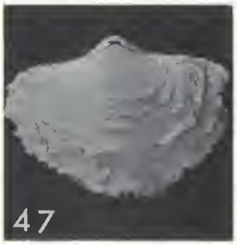
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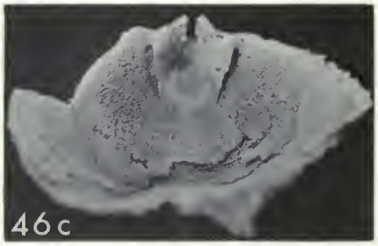
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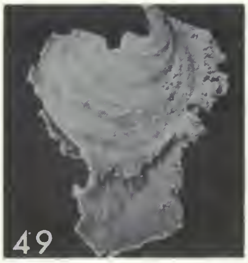
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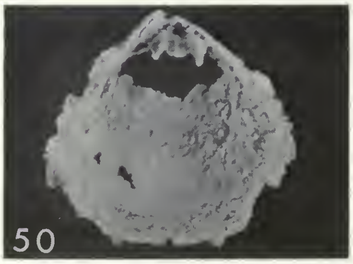
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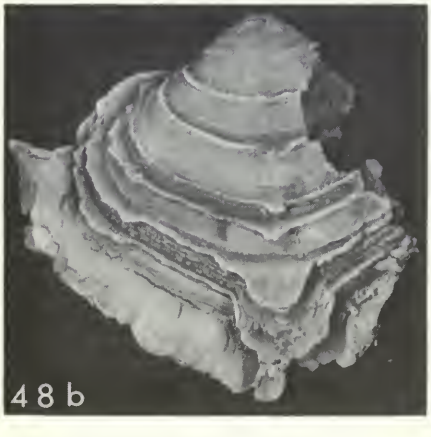
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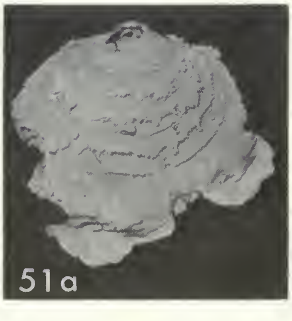
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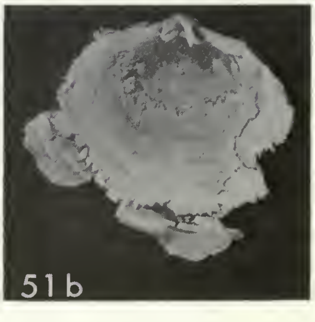
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the collections of the BM(NH), London, are clearly conspecific with the lectotype of *S. squamosa* Phillips. A neotype for *A. lamellosus* (BM(NH) B20138) was selected by Brunton (1980: figs 16a–d).

DESCRIPTION AND DISCUSSION. This species is uncommon in the silicified Fermanagh faunas, there being five more or less complete shells plus fifteen reasonably complete valves or conjoined umbones. Sizes range from a shell 4 mm wide to one approximately 23 mm wide, excluding the lamellose flanges. Incomplete silicification and the jointing of the rocks has led to some fragmentation during acid digestion. However, the preservation of long and delicate flanges (Fig. 49) indicates that the specimens were not moved any great distance before burial and there is little sign of crushing having taken place. The specimens are considered to be a sample of the brachiopod assemblage that lived in this area.

Descriptions of internal morphology are almost totally lacking for *Actinoconchus* species. Davidson (1882: 98; pl. 5, figs 14–19) described the spiralia of '*Athyris plano-sulcata* of Phillips', in specimens from Castleton, Derbyshire prepared by Rev. N. Glass; one of his figures is reproduced in the *Treatise* (Williams *et al.* 1965: H661, fig. 537.5a). Inspection of these Davidson specimens supports the figures he published. Regretably only one partially-preserved silicified spiralia pair is available, but this shows the hood-like jugum from which the short secondary spires project posterodorsally. It is impossible to be sure of the identification of the specimens prepared by Glass and assigned by Davidson to *A. planosulcata*, but this species and *A. lamellosus*, and possibly *A. paradoxus*, are known from the Castleton area of Derbyshire and as the spiralia of the Athyridinae all seem very similar the specific determination is probably of little consequence.

The silicified specimens of *A. lamellosus* retain well-preserved cardinalia. The cardinal process (Figs 44b, 45) projects posteroventrally into the ventral umbo and is confined laterally by deep sockets, the ridges of which merge posteriorly into the cardinal process and medially overhang the cavity leading to the small cardinal foramen. The structure lacks clear differentiation into hinge plates, socket ridges, etc. owing to its confined median position between the teeth. These are large and supported by well-developed dental plates (Fig. 44b) which became partially buried by secondary shell thickening during the later stages of ontogeny. The posterior dorsal adductor muscle scars are divided medially by a low myophragm. They are elliptical to rhombic in outline and bordered anteriorly by less well-defined elongate anterior scars (Fig. 45b). A pitted area, possibly marking the gonocoel, surrounds the muscle scars laterally and posterolaterally. The ventral adductor muscle scars are narrowly obovate and poorly differentiated medially. The diductor scars are less well-defined but extend widely anterolaterally, as illustrated by Weller (1914: pl. 78, fig. 3, reproduced in Williams *et al.* 1965: H661). Pitting, like that of the dorsal valve, occurs posterolaterally and the ventral valve umbo became progressively thickened on the outer sides of the dental plates until, in old shells, they became almost buried. Between the plates the umbonal cavity remains open and, in life,

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Figs 44–51 *Actinoconchus lamellosus* (Léveillé). Fig. 44a, b, umbonal regions of an adult specimen seen externally and internally; the close fit of the dorsal umbo below the ventral umbo can be seen and, internally, the articulation and cardinalia are well displayed, including the apical plate (arrowed) in the ventral umbo. BB43400, ×4. Fig. 45a, b, external and internal views of an almost complete dorsal valve showing the cardinal process, with its small foramen (arrowed), the adductor muscle scars and median myophragm (arrowed), and internal posterolateral ornamentation. BB63399, ×3. Fig. 46a–c, young ventral valve viewed externally, internally and posteroventrally to show the strong teeth and dental plates. BB63402, ×5, ×5 and ×6 respectively. Fig. 47, dorsal view of specimen from the Tournai region of Belgium. BM(NH) 64892, ×1. Fig. 48a, b, dorsal and ventral views of incomplete adult shell with well-preserved pedicle aperture and marginal shelly flanges. BB63398, ×2. Fig. 49, external view of incomplete juvenile ventral valve retaining a large portion of shelly flange medially. BB63403, ×5. Fig. 50, interior of juvenile dorsal valve showing the inner socket ridges, cardinal process (with its foramen), and a piece of ventral valve attached by its tooth on the left. BB63404, ×10. Fig. 51a, b, exterior and interior views of young dorsal valve showing lamellose ornamentation, and the cardinalia. BB63401, ×3.

accommodated the pedicle capsule. Apically, adjacent to where the cardinal process fits between the dental plates, the pedicle cavity of adult specimens has a small anteriorly-projecting plate (Fig. 44b) which would seem to have provided a separation between the pedicle capsule and the diductor muscles, where they were attached to the cardinal process. As the shell opened this little plate fitted closely into the posteromedian groove of the cardinal process.

Athyris bradyensis Carter (1967: 336), from Late Kinderhook limestones (high Tournaisian) of Texas, is similar to *A. lamellosus* externally and seems to have identical lamellose flanges. However, Carter's serial sections indicate a cardinal process different from that of the Fermanagh specimens, and he records a dorsal sulcus, especially in young specimens. A slight dorsal sulcation is normally only seen anteriorly on adult shells of *A. lamellosus*. Within the concepts of *Athyris* and *Actinoconchus* presented here, in which an attempt is made to revert to M'Coy's original definitions, *A. bradyensis* Carter would certainly be placed within *Actinoconchus*, and is closely allied to *A. lamellosus*.

The *Athyris lamellosus* described in the literature from Osagian formations in the central states of the U.S.A. does seem to be conspecific with the European species and may have developed from the older *A. bradyensis* stock of the southern states. If so *Actinoconchus lamellosus* (Léveillé) is known from North America in rocks of mid to upper Tournaisian age; from Britain and western Europe almost throughout the Tournaisian and Viséan, and is recorded from rocks, probably of high Viséan age, in the Moscow basin. Gaetani (1968) records the species from the Tournaisian of the central Elburz. The species has been recorded from China and Jin & Fang (1983) have used material from Yunnan province for the designation of a new genus, *Lamellosathyris*. These authors point out that their *L. lamellosa* lacks the radiating striations so characteristic on the flanges of *A. paradoxus* and that *Actinoconchus*, in their restricted sense, is not strongly folded. Until the Chinese specimens of *L. lamellosa* can be compared with well-authenticated *A. lamellosus* (Léveillé) it is impossible to evaluate *Lamellosathyris*. However, I have sympathy for their differentiation of *A. lamellosus* from *Actinoconchus* and drew attention to some of the differences in 1980 (pp. 225–6).

Genus ***CLEIOTHYRIDINA*** Buckman 1906

[= *Cleiothyris* King 1850: 137]

TYPE SPECIES. *Atrypa pectinifera* J. de C. Sowerby 1840, by original designation of King, 1850, for *Cleiothyris*, from the Permian of Co. Durham, validated by the I.C.Z.N. (1976). See Brunton (1980: 227) for details.

DIAGNOSIS (emended). Subequally biconvex athyridines with slight dorsal fold and ventral sulcus developed anteriorly. External ornamentation of lamellose growth lines bearing flattened spine-like frills.

DISCUSSION. Buckman (1906) established the genus *Cleiothyridina* as a new name for *Cleiothyris* King 1850. This being so the type species is that designated by King for *Cleiothyris, C. pectinifera* (J. de C. Sowerby) (Article 67i of the International Code of Zoological Nomenclature, 1964). This is a Permian species which was thought by some authors to be synonymous with the Carboniferous shell called *Athyris deroissyi* (Léveillé 1835). King remarked that the two bore a striking resemblance. It is probably because he thought the two synonymous that Buckman (1906: 234) designated '*Athyris Royssii*, Davidson, Mon. Carb. Brach. pl. xviii, fig. 8' as type species. Following Buckman the concept of *Cleiothyridina* has been based upon the species illustrated by Davidson (1861: pl. 18, fig. 8), quoted by Buckman, and called '*Athyris Royssii*'. Being somewhat conservative in his systematics Davidson placed several species, including *Spirifera fimbriata* Phillips 1836, into synonymy with '*Athyris Royssii* L'Eveillé', but noted in the plate explanation of pl. 18, fig. 11 that he there illustrated the original Phillips specimen of *S. fimbriata*. This specimen is preserved in the Oxford University Museum (E1093) and it is clear that Davidson's illustrations (1861) on pl. 18, figs 8–11 are of *fimbriata* Phillips, and not *deroissyi* Léveillé, a quite distinct species described and figured by Léveillé (1835: 39; pl. 2, figs 18–20). *Cleiothyridina fimbriata* (Phillips), previously commonly called *C. deroissyi* (Léveillé) (e.g.

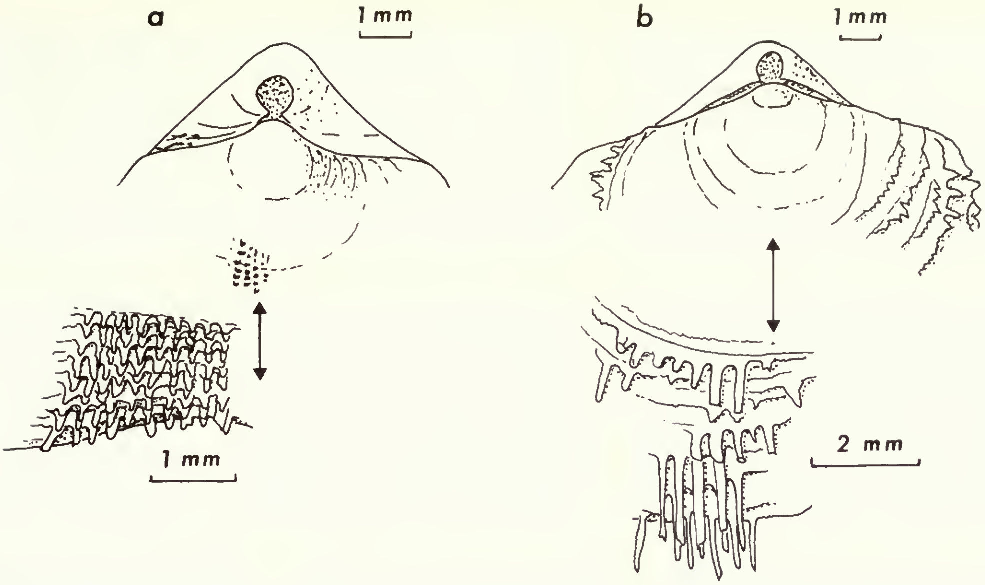


Fig. 52 Drawing comparing the umbonal morphologies and external ornamentations of (a) *Cleiothyridina deroissyi* and (b) *C. fimbriata*. Note the less prominent ventral umbo but stronger and more spine-like ornamentation on the latter (see Figs 62, 67).

Treatise, Williams *et al.* 1965), is closely comparable to the Permian species *C. pectinifera* (J. de C. Sowerby), the type species. Thus although the type species is here corrected to *pectinifera* (for long recognized by Russian palaeontologists), the concept of the genus remains unaltered. Had it been necessary to revert to *deroissyi* Léveillé as type species, the concept of *Cleiothyridina* would have altered, for the difference between *deroissyi* and *fimbriata* is much greater than between *fimbriata* and *pectinifera*. In the silicified Fermanagh faunas both *C. fimbriata* (Phillips) and *C. deroissyi* (Léveillé) are found (Fig. 52).

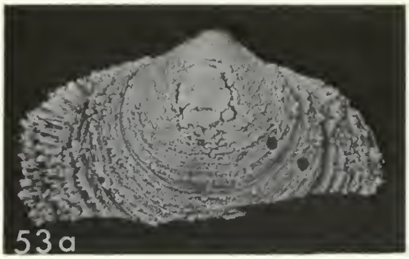
The I.C.Z.N. (1976) has validated the generic name *Cleiothyridina*, type species *C. pectinifera* (J. de C. Sowerby), and accepted the specific names *fimbriata* Phillips and *deroissyi* Léveillé (Brunton 1972: 142).

Cleiothyridina differs from other Lower Carboniferous Athyridinae in its external ornamentation of concentric, long, spine-like shelly frills. In examples of *C. fimbriata* and *C. pectinifera* these frills are differentiated, especially anteromedially on adult shells, into distinct 'spines' which appear to have had hollow centres. The cardinalia also differ from other Athyridinae in having the cardinal process well differentiated from the hinge plates; in *Actinoconchus* the two are ill-defined and the cardinal process of *Composita* is distinctive. Representatives of *Cleiothyridina* are widely distributed through Lower Carboniferous to mid Permian strata.

Cleiothyridina fimbriata (Phillips)
Figs 53–66

v* 1836 *Spirifera fimbriata* Phillips: 220 (no figs).
1843 *Terebratula plano-sulcata* (Phillips); de Koninck: 301 (*pars*); pl. 21, figs 1e, f.
v. 1861 *Athyris Royssii* (Léveillé); Davidson: 84 (*pars*); pl. 18, figs 8-11 (fig. 11 from Phillips' original specimen).
v. 1863 *Athyris Royssii* (Léveillé); Davidson: pl. 54, fig. 8.

Diagnosis. Subcircular to transversely broadly obovate in outline, anterior commissure rectimarginate. External ornamentation of concentric thin shell lamellae separating into long recumbent spinose frills.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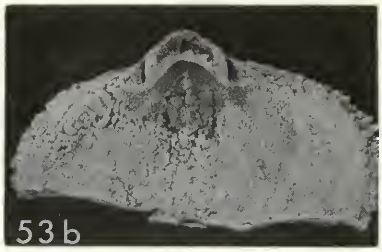
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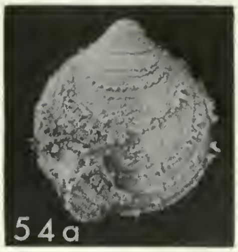
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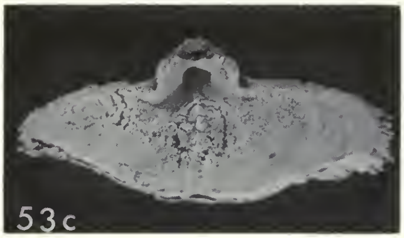
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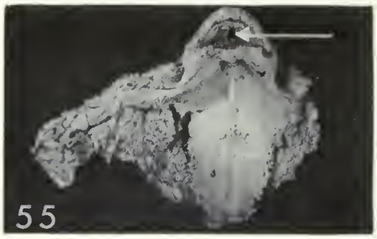
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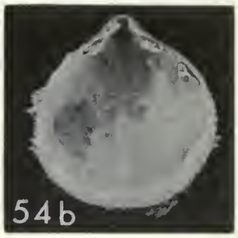
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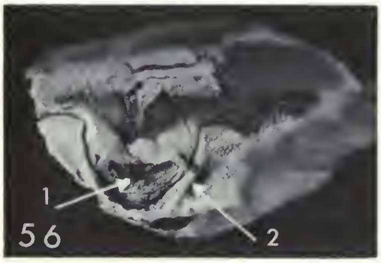

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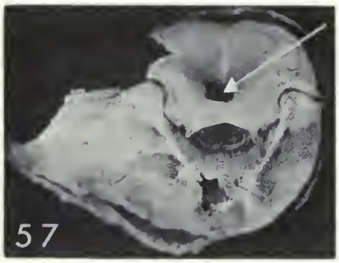
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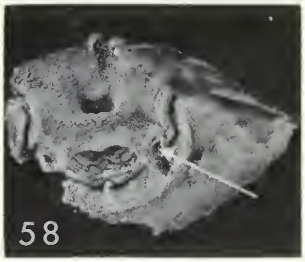
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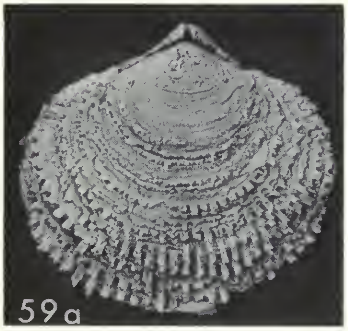
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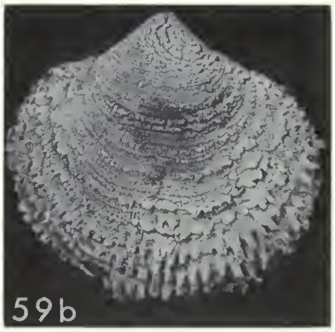
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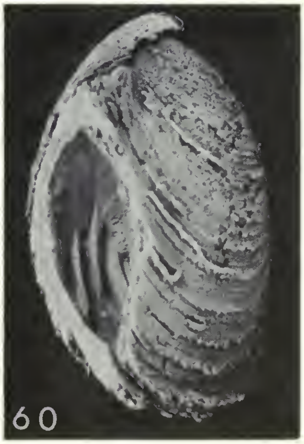
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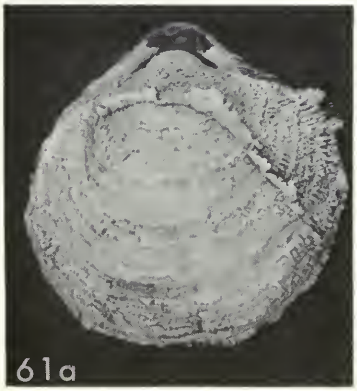
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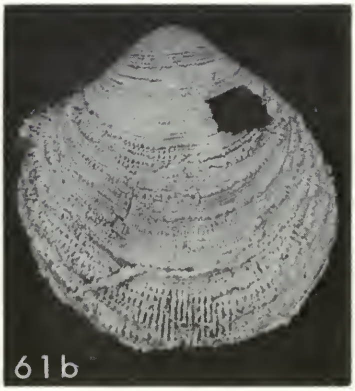
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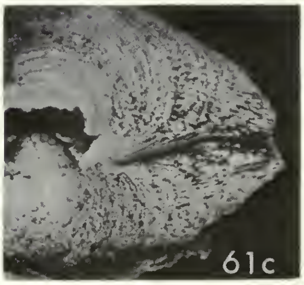

61c

Lectotype. *Spirifera fimbriata* Phillips, Phillips collection, Oxford University Museum, E1093. From the Lower Carboniferous near Florence Court, Co. Fermanagh, Ireland, probably of early Asbian age (sel. Brunton, 1980: 228).

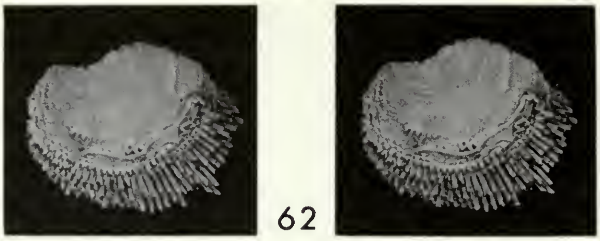
Description. When stripped of its spinose ornamentation the shell is more or less circular in outline, but preservation of these frills commonly adds to the width of the outline posteriorly (Fig. 53a). The umbones are incurved, that of the ventral valve being pointed whilst the dorsal umbo, in all but young shells, is enclosed within the wide, open delthyrium (Fig. 60). In this way the dorsal umbo projected into the ventral valve which the shell was open. In large specimens a short and narrow, flattened, pseudo-interarea may be developed on ventral valves. The commissure is rectimarginate but rarely there is a slight uniplication. Growth lines are marked over the entire shell. Posteromedially the spinose ornamentation is commonly lacking, but peripherally preservation may be good. Each growth line is extended as a thin shelly sheet for a fraction of a millimetre before differentiating into flattened spine-like outgrowths reaching at least 5 mm in length (probably these were much longer while the brachiopod was alive) (Fig. 59). Peripherally, and especially anteromedially (Fig. 62), the 'spines' are well developed and seem to have grown with hollow centres, but no hollow connections to the inner surfaces of the valves were retained. The 'spines' are connected laterally by extremely thin sheets of shell fibres. Posteriorly, lateral to the umbones, the spinose ornamentation is lacking on those regions of the valves which would have impinged against one another when the shell opened (Fig. 61c).

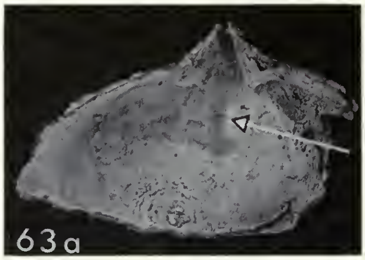
The valve interiors are typically athyridacean. Ventral valves have short dental plates (Fig. 63b), which tend to become buried by secondary shell during late stages of ontogeny, supporting dorsally-projecting, stubby teeth (Fig. 57). Adductor and diductor muscle scars are poorly impressed, the former being narrowly ovate and the latter spreading anterolaterally.

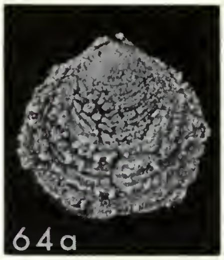
The dorsal cardinalia are approximately one quarter of the total width of the shell. The inner socket ridges curve medially from the valve surface, then ventrally, and their outer surfaces continue ventromedially to form the outer surface of the transversely hemielliptical cardinal process (Figs 53, 55). When the shell is closed the cardinal process fits snugly between the dental plates, within the ventral umbo, and the ridged myophore faces anteroventrally (Figs 56, 58). The short inner hinge plate is entire and recedes posteriorly, but is well differentiated from the sockets and cardinal process. Posteriorly, at the base of the cardinal process, is a small median foramen leading to the cavity dorsal to the hinge plate (Fig. 58). Narrow crura extend anteroventrally from the inner sides of the socket ridges; i.e. there are no well-differentiated outer hinge plates. The dorsal diductor muscle scars form elliptical, slightly sunken areas separated by a low ridge which merges anteriorly into a shallow groove, separating thickened areas of shell. These possibly represent the sites of mantle canals.

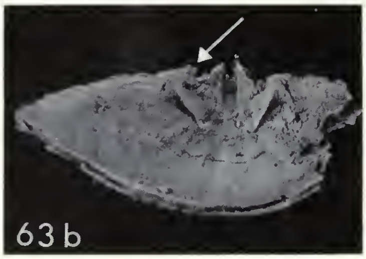
The external dimensions of the 28 sufficiently well preserved Fermanagh specimens are given on Fig. 66, on which are also plotted the dimensions of the lectotype.

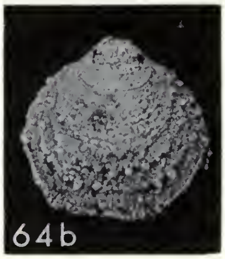
Figs 53–61 *Cleiothyridina fimbriata* (Phillips). Fig. 53a–c, exterior and interior views of incomplete adult dorsal valve, showing external ornamentation and the cardinalia. BB62976, ×3. Fig. 54a, b, exterior and interior of juvenile ventral valve showing the pedicle aperture and large teeth. BB63454, ×6. Fig. 55, internal view of adult cardinalia, with foramen (arrowed) and adductor muscle fields separated by a low myophragm. BB63451, ×4·5. Fig. 56, internal posterior view of conjoined umbones, showing the close fit of the cardinalia between the adult dental plates; the cardinal process myophore, and foramen, is arrowed (1), as is the crus on the right side (2). BB63447, ×4. Fig. 57, another set of conjoined adult umbones showing the dorsal cavity (arrowed) connecting to the foramen on the myophore surface of the cardinal process. BB63449, ×4. Fig. 58, a pair of umbones from an old specimen in which the dental plates are almost buried by secondary shell; the broken crura are visible (arrowed on the right). BB63450, ×5. Fig. 59a, b, young complete shell viewed dorsally and ventrally, displaying the spinose ornamentation and close fit of the umbones externally. BB63452, ×3. Fig. 60, lateral view of incomplete shell showing part of the spiralia inside. BB63446, ×4. Fig. 61a–c, adult specimen viewed dorsally, ventrally and posteriorly; the ventral umbo is broken, allowing the dorsal umbo to be seen tucked within its cavity. BB63445, ×2.

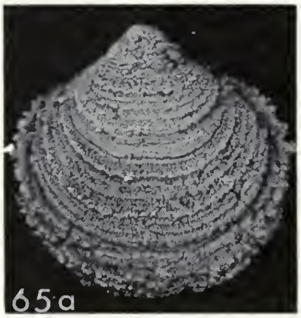


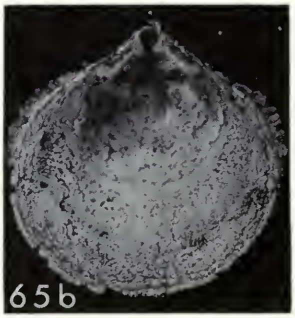












Figs 62–65 *Cleiothyridina fimbriata* (Phillips). Fig. 62, a stereoscopic pair illustrating the spinose ornamentation on an incomplete ventral valve. BB62975, ×2·5. Fig. 63a, b, internal views looking ventrally and posteriorly in an incomplete young ventral valve, lacking thickening around the dental plates; the cyrtomatodont teeth show, one throwing its typical shadow to the valve floor (arrowed). BB63448, ×4·5. Fig. 64a, b, dorsal and ventral views of juvenile shell. BB63455, ×6. Fig. 65a, b, external and internal views of young ventral valve. BB63453, ×5.

Discussion. The first illustration we have of *C. fimbriata* (Phillips) is that of Davidson (1861: pl. 18, fig. 11). Davidson commonly restored the appearance of the specimens he figured and this is true of this particular illustration, as can be seen by comparing it with his original drawing (vol. 10 of Davidson's drawings in the BM(NH)). This original drawing, annotated by Davidson as being 'in Phillips Collection marked fimbriata No. 202', compares very closely with a specimen in the Phillips collection of the Oxford University Museum (E1093), the specimen designated as lectotype (see Brunton 1980: fig. 19a, b). This Phillips specimen came from 'Florence Court'

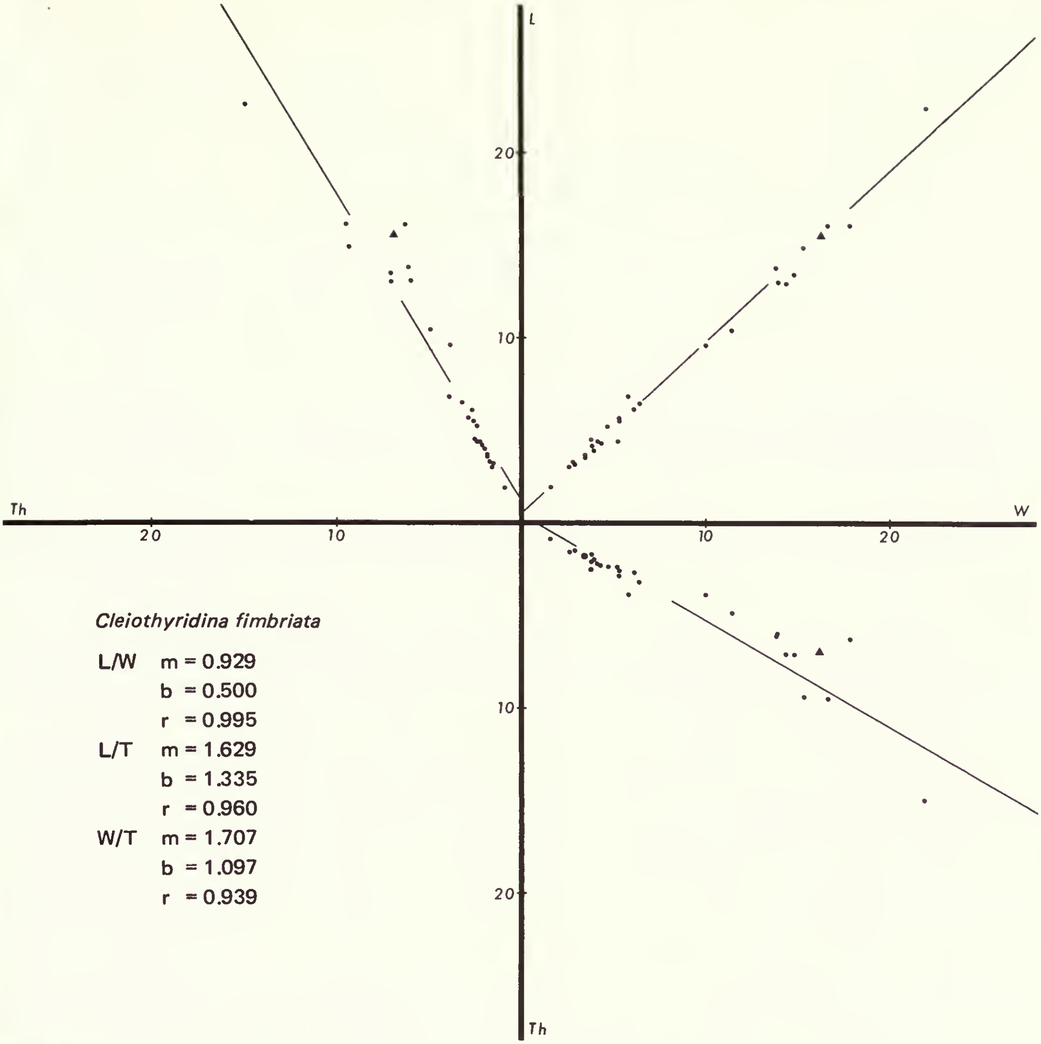


Fig. 66 *Cleiothyridina fimbriata* (Phillips). Length, width and thickness plots of 28 specimens from Co. Fermanagh, plus the lectotype (▲) also from Co. Fermanagh. m = slope of regression line; b = intersection point of m with the axis; r = coefficient of correlation.

(Phillips 1836: 220) in Co. Fermanagh, about 13 miles SSE of the main collecting locality for the silicified material described here. The actual locality of the specimen is unknown, but it is likely that it was collected from the well-exposed Glencar limestones and shales of the Cladagh river, about 3 miles west of Florence Court. In all known respects the specimen is conspecific with the sample population described here.

Since the publication of Davidson's (1861) fine illustrations of this species, unfortunately misidentified as *C. deroissyi* (Léveillé), the name *fimbriata* has largely gone out of use. George (1932), believing there was no foundation for the species and that *S. fimbriata* Phillips was probably a *Reticularia* sp. close to *R. imbricata* (Sowerby), argued that the 'name be discarded'. If it were not for Davidson's good, if somewhat embellished, illustration of the type specimen, which still exists, this would be a sensible suggestion. But in view of the above facts and the need to return to Léveillé's original concept of *S. deroissyi*, the author follows Ramsbottom (1969: 10) in retaining Phillips' species. Thus Phillips' name *fimbriata* is here used to describe specimens hitherto commonly named as *deroissyi* and often cited incorrectly as being the type species of *Cleiothyridina*.

The most striking feature of *C. fimbriata* is its spinose external ornamentation (Fig. 62). During ontogeny these spine-like structures increased in both girth and length. On larger shells (20 to 25 mm long) there are at least 50 to 60 growth lines from which the spinose lamellae extended, at least during the life time of the animal (Davidson 1861: 85 records up to 80 of these lamellae). More rapid shell growth during early ontogeny resulted in more widely spaced growth lamellae on the umbonal regions than anteriorly. This wider spacing, together with the maximum time for abrasion during life, results in the umbones normally being bald. The best 'spines' were developed late in life, and anteriorly individual 'spines' measure about 0·3 mm in width close to their base, and taper very gradually for a length of at least 5 mm. In the silicified material these largest 'spines' are hollow, but this may be a silicification phenomenon and remains to be demonstrated in unaltered specimens.

Rare variants occur in which the spine-like processes are very fine (*c.* 0·1 mm wide) and thus less well differentiated from the intervening extremely delicate shelly lamella, which seems to be composed of a single layer of long secondary shell fibres. At present there is no evidence that this variation is other than intraspecific.

The orientation of the spinose lamellae altered during ontogeny and differs with respect to the two valve surfaces. On ventral valves the lamellae and 'spines' extend at a more or less constant low angle from the external valve surface so that at the anterior margin of adult shells the 'spines' project anterodorsally. On the dorsal valve these lamellae project from the surface at an increasingly higher angle from the umbo to the anterior margin where the 'spines' also project anterodorsally, parallel to those of the ventral valve. They did not, therefore, interlock around the commissure when the shell was closed, but formed a closely fitting flange or corona extending from the valve margins.

FUNCTIONAL MORPHOLOGY. These brachiopods were pedunculate, attached to the substrate by a thin pedicle which probably 'rooted' into sediment rather than onto hard fragments of detritus or pebbles. None of the silicified specimens shows signs of umbonal distortion or undue abrasion (Figs 54, 59), as commonly occurs on specimens attached to hard surfaces by a pedicle. The spinose lamellae formed marginal flanges throughout ontogeny and probably helped in the maintenance of a sediment-free brachial cavity, in a fashion similar to that postulated by Shiells (1968) for *Kochiproductus*.

In rare instances there is evidence, from silicified material in which the external ornamentation is preserved posteriorly, of the degree to which these shells could have opened. In such shells the lamellae lateral to the umbones are sparsely developed, especially on the ventral valve (Fig. 61a, c). This relatively smooth area is that over which the dorsal valve moved, as the shell opened, and indicates a gape of up to about 20°. This compares with gape angles of about 15° and 20° respectively for dead shells of the Recent *Hemithyris psittacea* (Gmelin) and *Terebratella dorsata* (Gmelin). The teeth and sockets are relatively open anteriorly but the teeth are typically cyrtomatodont (Jaanusson 1971), being recurved posteriorly as a result of posterior resorption of the previously-developed shell material of the teeth (Fig. 63b). As Jaanusson (1971) stated, these posteromedially-protruding, hook-shaped teeth are typical of Rhynchonellida. Spiriferida and Terebratulida, tended to hold the two valves strongly together and limited the degree to which the shell could open. In *C. fimbriata*, and other athyridaceans, posterior resorption of the teeth was necessary to allow the dorsal umbo free movement into the ventral umbo when the shell opened.

RANGE. *C. fimbriata* is known from Lower Carboniferous rocks throughout the British Isles, but seems not to have extended far into Europe. Closely related species occur in the Lower Carboniferous of Russia, the Elburz, Iran (e.g. *C. kusbassica* Besnossova 1963) and in the south-western states of the U.S.A. (e.g. *C. glenparkensis* Weller or *C. sublamellosa* (Hall)).

In the British Isles the species ranges through late Tournaisian and Viséan strata and the related species mentioned above from Russia and North America are found in rocks mostly equivalent in age to Tournaisian. The species may be found in argillaceous limestones, as in the silicified Fermanagh faunas, shales or, less commonly, associated with the so-called 'reef' limestones. It seems to have tolerated a soft sea floor composed of fine silt to mud grade sediment. In the silicified faunas it occurs about twice as commonly as *C. deroissyi* and with a larger proportion of young shells.

Cleiothyridina deroissyi (Léveillé)
Figs 67–73

1835 *Spirifer De Roissyi* Léveillé: 39; pl. 2, figs 18–20.
1843 *Terebratula Royssii* (Léveillé) de Koninck (*pars*): 300; pl. 21, figs 1a?, 1b–d.
1851 *Terebratula squamigera* de Koninck: 667; pl. 56, figs 9a–d.
1887 *Athyris Roissyi* (Léveillé) de Koninck: 85; pl. 19, figs 28, 29.
1887 *Athyris squamigera* de Koninck: 82; pl. 20, figs 16–22.
? 1914 *Cleiothyridina prouti* (Swallow); Weller: 474; pl. 79, figs 13–16.

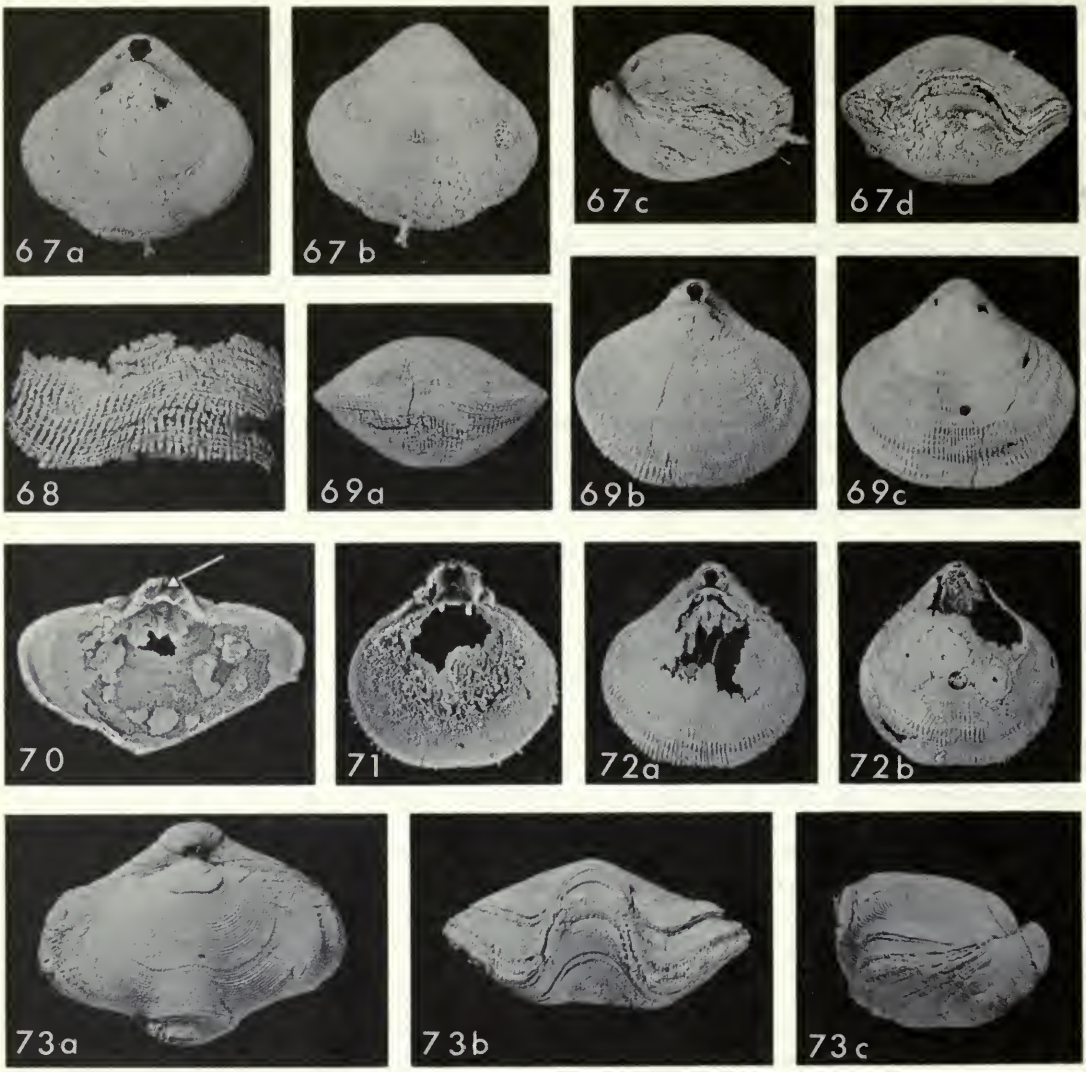
Diagnosis (emended). Circular (young) to transversely elliptical in outline, strongly biconvex shells. Dorsal fold and ventral sulcus persistent, forming strong parasulcate anterior commissure. External ornamentation of closely-spaced growth lines from which extend radially-arranged spinose lamellae, which, when preserved, form a dense mat.

Neotype. Léveillé's specimens appear to be lost. A lectotype of *A. squamigera* de Koninck has been selected (Brunton 1980: 229), which is thought to be conspecific with *deroissyi*. This specimen is here selected neotype of *Spirifer deroissyi* Léveillé.

Description. Adult shells are unusually transverse for the genus and, with a thickness exceeding half the shell width, are thicker than *C. fimbriata*. The strong parasulcate anterior commissure results from a fold and sulcus which persisted throughout ontogeny (Fig. 67d). Both umbones are incurved, the dorsal being tucked below the ventral umbo, in which is a circular pedicle foramen opening anteriorly to the wide delthyrium bordered by low ridges (Fig. 69b). There is no true interarea, but on larger shells the posterior margin of the ventral valve may be flattened as a result of the movement of the valves against each other as the shell opened and closed.

The external ornamentation developed throughout ontogeny, but is normally fully preserved only towards the margins of the valves. Short lamellose growth lines developed at regular and frequent intervals (about 5–7 per mm) throughout ontogeny, from which grew radially-aligned, flattened, spine-like projections, commonly giving the growth lines a serrated appearance (Fig. 69). When fully developed these outgrowths formed a dense 'mat' in which the 'pile' lay oblique to the valve surface and formed an extension to the valve margins (Fig. 68). For the two sets of spinose lamellae to meet parallel to each other at the anterior commissure, those of the ventral valve projected at an increasingly high angle from the valve surface during ontogeny. On large specimens the lamellae are subparallel to the ventral valve surface posteriorly, but may be perpendicular to the surface near the anterior margin. The mat-like pile appears to have originated close to the valve surfaces from the shelly fibres, which constitute the lamellae, separating laterally from median bundles of fibres. These formed the distally diminishing spinose elements of the lamellae. In this way spinosity is lost distally and the valve surface appears to be covered by a dense needle-like pile. On the silicified Fermanagh specimens normally only the radially-arranged spinose lamellae remain (Fig. 72). It is not known whether the lack of complete ornamentation results from abrasion prior to silicification, non-silicification of the needle-like pile, or loss of this structure during acid development. However, a combination of the first two is suspected.

The ventral valve is furnished with slightly hooked cyrtomatodont teeth supported by short dental plates, which do not extend anteriorly from the umbonal cavity, except immediately below the teeth. The intersection of the tooth and supporting plate is marked posteriorly by a narrowly triangular shelf just below the margins of the delthyrium, a region in which some resorption of the teeth must have taken place during ontogeny. The paired adductor scars are more or less elliptical in outline, close to the mid-line and sunk below the internal shell surface. The diductor scars are poorly differentiated and have not been clearly distinguished.



Figs 67–73 *Cleiothyridina deroissyi* (Léveillé). Fig. 67a–d, complete shell viewed dorsally, ventrally, laterally and anteriorly. BB63461, ×2. Fig. 68, fragment of a ventral valve with well-preserved ornamentation. BB63466, ×4. Fig. 69a–c, young shell viewed anteriorly, dorsally and ventrally; the radially-aligned spinose lamellae can be seen, and the ventral valve is bored medially. BB63462, ×2·5. Fig. 70, dorsal valve interior, looking posterodorsally to show the cardinal process, foramen (arrowed), and sockets. BB63464, ×2·5. Fig. 71, juvenile dorsal valve interior with teeth and umbo of the ventral valve remaining attached; the crura extend from the edge of the hinge plate. BB63465, ×6. Fig. 71a, b, incomplete young shell viewed dorsally and ventrally; the ventral valve is bored medially. BB63463, ×3. Fig. 73a–c, adult shell from the Tournai region of Belgium, viewed dorsally, anteriorly and laterally. BM(NH) 65002, ×1.

The cardinalia are not heavily calcified and seem to vary quite considerably in absolute and relative size compared to the valve width. There is insufficient material to allow a full study of this feature, but in two Belgian specimens of about 17 mm and 20 mm width the cardinalia measure 3·5 mm and 5·0 mm respectively, between the bases of the inner socket ridges. The largest Fermanagh dorsal valve is 15 mm wide with cardinalia 5 mm wide. The cardinalia width is obviously linked to the distance between the teeth and the width of the delthyrium. The crural bases, hinge plates and foramen are illustrated in Fig. 70, in which it can be seen that the cardinal process is much smaller than that of *C. fimbriata*, and it may be that the diductor muscles were unusually slight, leaving little trace in either valve. The dorsal adductor scars are broadly elliptical in outline, separated medially by a low ridge and are slightly sunken. Otherwise the valve interiors are smooth.

DISCUSSION. In the acid-developed Fermanagh faunas there are 30 reasonably complete shells and valves of *C. deroissyi* (about half the number of *C. fimbriata* specimens).

C. fimbriata differs from *C. deroissyi* (Léveillé) both externally and internally. The most obvious differences are shell shape and ornamentation; *C. deroissyi* is a more transverse shell than *C. fimbriata*; it is thicker and the anterior commissure is strongly uniplicate as a result of a fold and sulcus, both of which originated close to the umbones.

The pedicle foramen is large and the umbones less incurved than in *C. fimbriata*. The external ornamentation contrasts with that of *C. fimbriata* in being much finer; growth lines are ill-defined, close together and regularly spaced and from them extend short, radially aligned, spinose lamellae. As in *C. fimbriata* the spinosity increases anteriorly, but never on *C. deroissyi* are long discrete spines preserved. The cardinalia of *C. deroissyi* differ in having a low cardinal process and gently arched conjoined inner hinge plates, with a large triangular foramen posteriorly.

The nomenclatorial history of *C. deroissyi* (Léveillé) is vexed. The original description (1835) is brief, but the three illustrations are characteristic in all respects, save for a lack of information upon the external ornamentation. De Koninck (1843) described and figured specimens under this name, some of which agree with Léveillé's description, others of which should probably have been referred to *C. fimbriata* (pl. 21, figs 1g, h). Subsequently (1851, 1887) de Koninck called *fimbriata*-like specimens *deroissyi* and put up a new name, *squamigera*, for specimens which should have been called *deroissyi* Léveillé. Davidson (1861) perpetuated the name *deroissyi* for specimens of *C. fimbriata* (Phillips). This incorrect use of the name *deroissyi* for a distinctive and fairly common western European athyridacean led to its adoption as the type species of *Cleiothyridina*, a course which has been challenged for many years by the Russians and more recently by Carter (1967), and which is here corrected (p. 57). Within the collections of the BM(NH) are specimens from de Koninck's collection named '*Terebratula squamigera* de Kon.' in his own handwriting (Fig. 73). These, and several other specimens from the Tournai area of Belgium, are relatively wider and thicker compared to their length than are the Fermanagh shells, but in other respects, such as details of ornamentation, cardinalia and articulation, they appear to be identical. From the growth lines on the Belgian shells it is clear that the length: width ratio remained fairly constant during ontogeny. The width of these shells did not, therefore, result from allometric growth in which width exceeded length only late in ontogeny. This partially silicified Belgian material is probably of Tu2 (C_1) age; the Fermanagh specimens are judged to be Viséan (Asbian, $D_1 \equiv$ V3b). A Tournaisian specimen from the Bristol area is like the Belgian specimens in shape and it may be that the species became relatively narrower, thinner and less sulcate during the Carboniferous.

The large athyridaceans from Belgium, reaching about 35 mm in length, are perhaps referable to *Athyris ingens* de Koninck (1887: 83); they appear to be a group of brachiopods showing characteristics intermediate between those of *C. deroissyi* and *C. fimbriata*. The external ornamentation is essentially *fimbriata*-like, and the size of the shell is more in keeping with this species. The strongly uniplicate anterior commissure is more reminiscent of *deroissyi*, but this folding only developed at about half the full valve length, and it could be argued that had *C. fimbriata* shells grown to this size they might have become similarly folded. Should this prove to have been the case, *C. ingens* should be considered as a large variant of *C. fimbriata*. It may be that the rare large specimens illustrated by Davidson (1861: pl. 18, figs 1–4) as '*A. Royssii*' (more correctly *C. glabristria* (Phillips)) should belong in this group, and that *C. glabristria* is a *C. ingens* stripped of its external ornamentation.

The pedicle foramen seems to have remained relatively large and accessible throughout ontogeny and it may be that this species relied upon its pedicle attachment to the substrate to a greater extent than did *C. fimbriata*. The small cardinal process myophore and indistinct ventral valve diductor muscle scars may indicate relatively long, thin diductor muscles, or a diductor system requiring less muscular energy to operate than in other thinner-shelled species, or both.

RANGE. *C. deroissyi* (Léveillé) occurs relatively commonly in the Tournaisian of Belgium but rarely in rocks of similar age in the British Isles. The species extends up through the mid-Viséan in Britain. *C. prouti* (Swallow) is a closely similar species from the Tournaisian (Fern Glen) of the south-western U.S.A.

Family **NUCLEOSPIRIDAE** Davidson 1881

Genus ***NUCLEOSPIRA*** Hall 1859

TYPE SPECIES. *Spirifer ventricosus* Hall 1857 from the Devonian Lower Helderberg group of New York State.

DISCUSSION. The genus is seldom recorded from Lower Carboniferous rocks, other than those of the Mississippi valley, U.S.A., where it appears to be confined to rock of Tournaisian age. The genus reappears in uppermost Mississippian rocks (= Namurian) of Montana, U.S.A.

Nucleospira carlukensis (Davidson)

Figs 74, 76–82

v* 1859 *Spirifera carlukensis* Davidson: 59; pl. 13, figs 14, 14a, b.
not 1863 *Spirifera carlukensis* Davidson: pl. 55, figs 14, 15.

DIAGNOSIS. *Nucleospira* with slight median sulcation on ventral valve, anterior commissure weakly uniplicate. Microspinous external ornamentation on both valves. Large tapering cardinal process with bifid tip curving posteroventrally into ventral valve umbo. Median ridges in both valves low.

LECTOTYPE. *Spirifera carlukensis* Davidson, Davidson collection figured 1859: pl. 13, figs 14, BM(NH) B7627, here selected as Lectotype. From the Hosie Limestone (late Viséan) of Hillhead, near Carluke, Lanarkshire (Fig. 77).

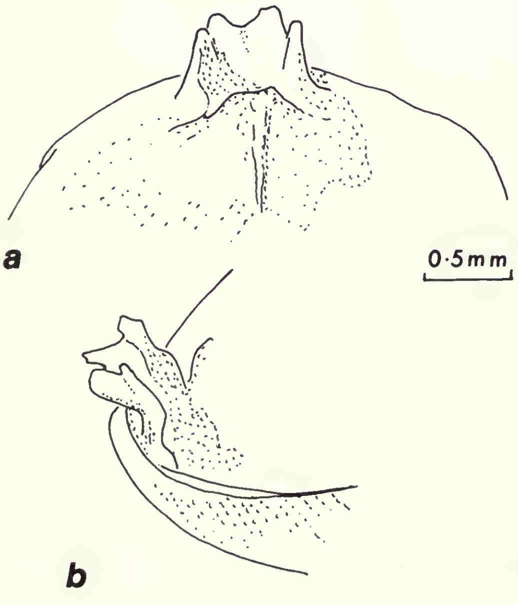


Fig. 74 Drawings of the cardinalia of *Nucleospira carlukensis* viewed (a) posterodorsally and (b) laterally, to show the large hooked cardinal process. (See also Fig. 80a, c).

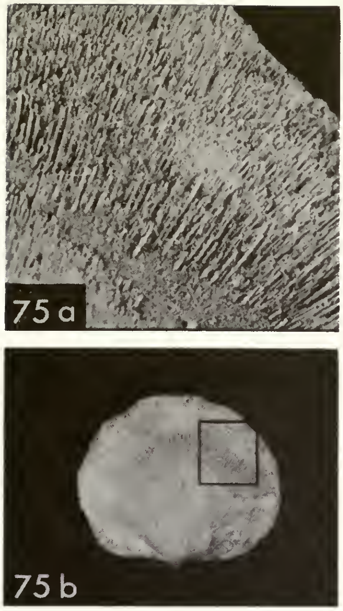
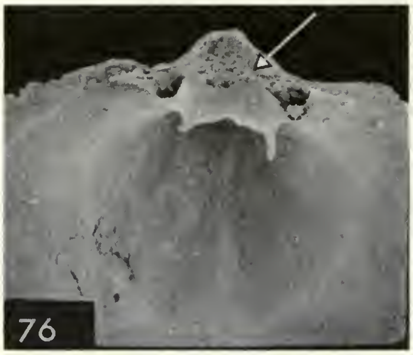


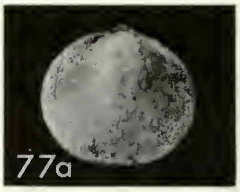
Fig. 75 The external microspinose ornamentation on the dorsal valve of *Nucleospira concinna* Hall, from the mid-Devonian of Wadsworth, New York, U.S.A. BB19736, (a) ×10, (b) ×1·5.

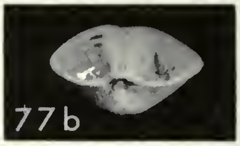
Description. The species is small (commonly about 5 mm wide, but reaching about 10 mm wide), circular to transversely broadly elliptical in outline and equibiconvex in profile. The hinge line is 2·0 to 2·5 mm wide in shells 5–8 mm wide. The ventral interarea is apsacline, slightly concave and with an open, relatively wide delthyrium. The dorsal umbo is prominent, but an interarea is lacking. The ventral valve commonly has a shallow median sulcus forming a weakly uniplicate anterior commissure. Both valves are ornamented with irregularly, but commonly anteriorly concentrated, growth lines and concentrically arranged fine spines of irregular diameter (Brunton 1976: pl. 115). The spines project radially, at high angles from the valve surfaces, with a frequency of 15–20 spines per mm measured along a growth band; they have not been observed more than about 0·3 mm in length (Fig. 79). The teeth are short and crytomatodont in character. There are no dental plates but the delthyrial margins are thickened (Fig. 81a). A low median ridge extends from the umbonal cavity nearly to the anterior margin, posteriorly dividing the weakly-impressed muscle scars; the adductor scars are elliptical in outline, restricted to the umbonal cavity and enclosed laterally and anteriorly by wide diductor scars which may extend for nearly one-third of the valve's length.

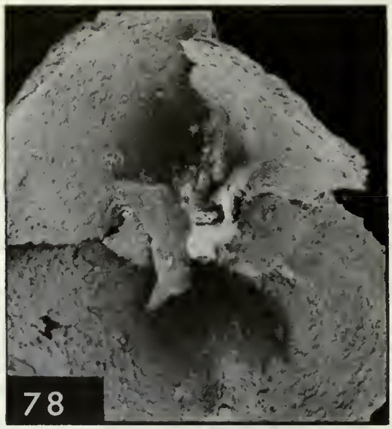
The dorsal valve interior is typified by the ventroposteriorly-projecting, hook-like cardinal process (Fig. 80). The sockets are small and the differentiation between the inner socket ridges, flanks of the cardinal process and crural bases is poor (Fig. 74). The floor of the socket curves ventrally without interruption, to form the crural base and flank of the cardinal process. The crura extend anteroventrally about midway between the socket and tip of the cardinal process (Figs 78, 82), which is bifid. The cardinal process is concave posteroventrally and its external (posterior) surface effectively seals the delthyrial opening; the myophores are situated distally on the ventrally- to ventroposteriorly-facing surfaces. Thus, with the exception of the crura, the whole cardinalia played a direct role in the articulation of the shell (Fig. 78), the teeth articulated against the posterolateral surfaces of a structure combining the functions of inner socket ridges and cardinal process base. A low median ridge extends from the dorsal umbonal cavity for at least half the valve's length. The adductor scars are narrowly ovate and positioned posteriorly adjacent to the median ridge; from their anterior margins extend the raised impressions of the 'vascula media'.

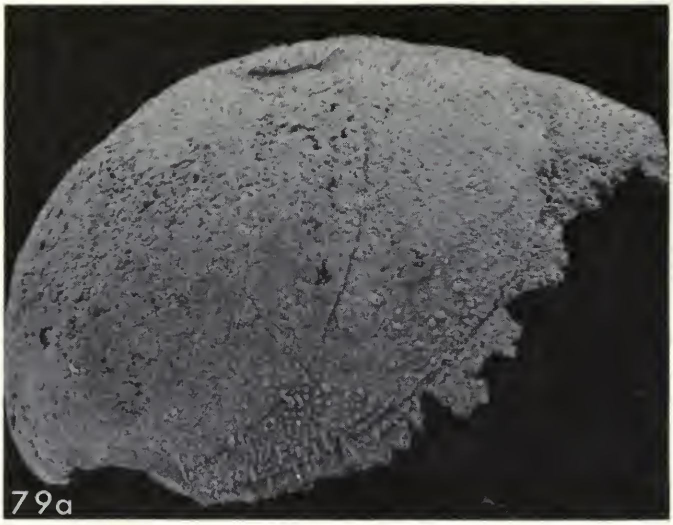
Discussion. In 1859 Davidson utilized two spellings for this species: the plate explanation (and labels on his specimens in the British Museum (Natural History)) being spelt '*carlukiensis*'. The

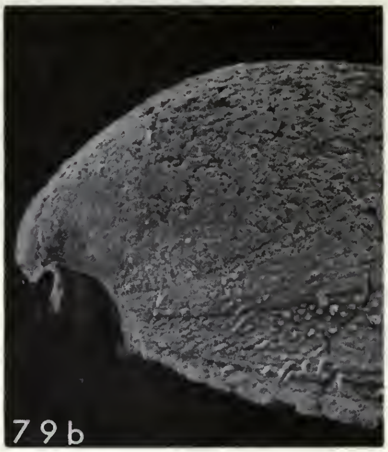


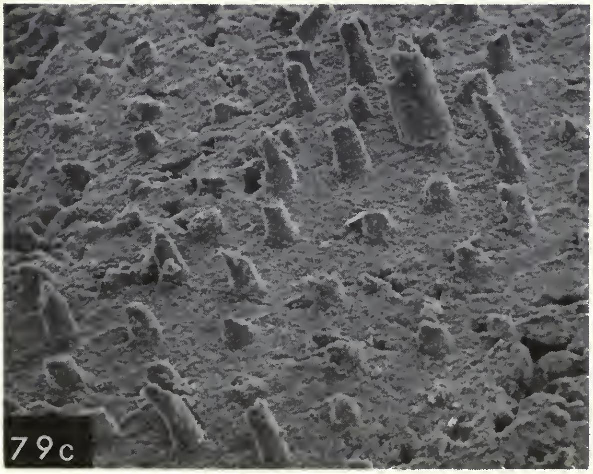


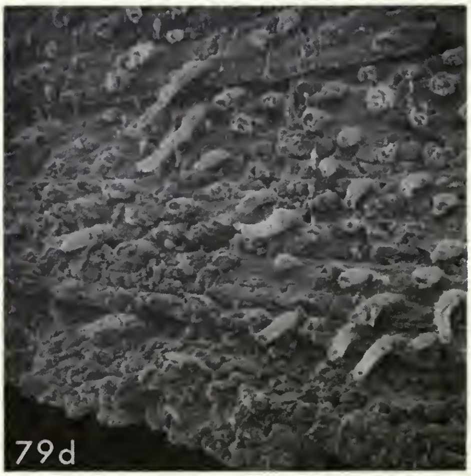




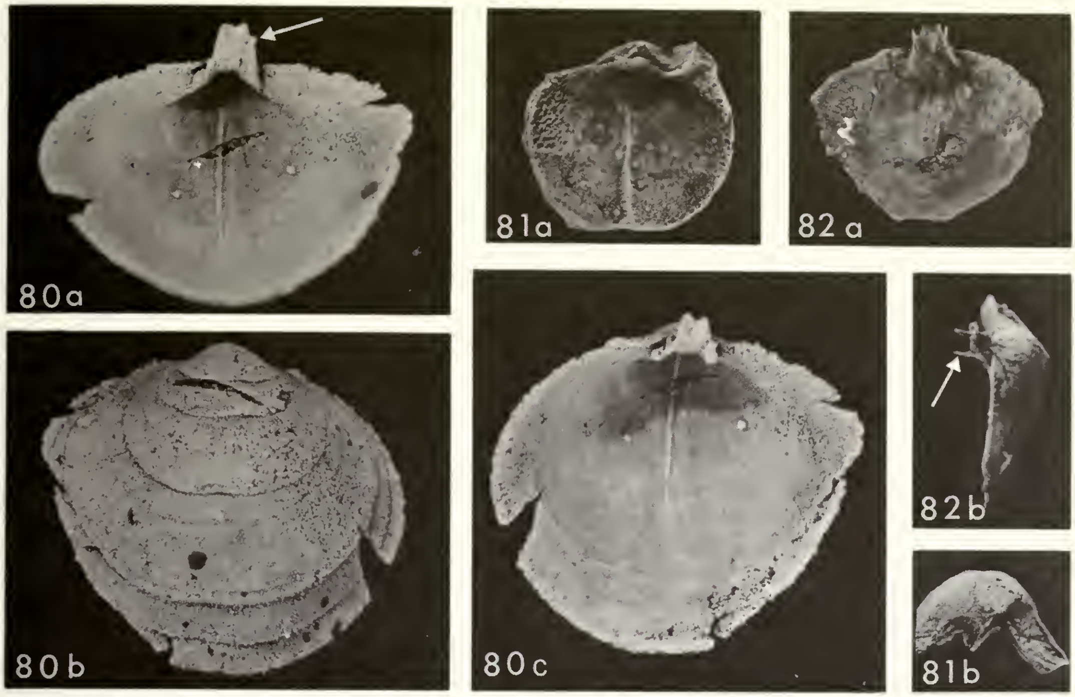








Figs 76–79 *Nucleospira carlukensis* (Davidson). Fig. 76, internal view of the posterior region of a ventral valve, in the delthyrium of which is fitted the cardinalia: their broken surface is arrowed and the crura project above the muscle scars on the valve floor. BD113, S.E.M. ×25. Fig. 77a, b, **lectotype** (herein selected), from the late Viséan near Carluke, Lanarkshire, viewed ventrally and posterodorsally. B7627, ×4. Fig. 78, pair of slightly crushed umbo interiors. The dorsal valve (uppermost) shows the left socket and half the cardinal process curving ventrally towards the ventral umbo; the cardinal process and other socket are broken in the whiter areas. BD115, ×25. Fig. 79a–d, ventral valve in lateral and slightly posterolateral views showing the interarea, delthyrium and some of the microspinous ornamentation, with details of the microspines anteromedially and posterolaterally. BB61625, S.E.M. (a) ×25, (b) ×40, (c), (d) ×150.



Figs 80–82 *Nucleospira carlukensis* (Davidson). Fig. 80a–c, dorsal valve viewed posterodorsally, externally and dorsally, to show the external ornamentation and internally, the cardinal process with its lateral crural bases and the median ridge. BB63458, ×6. Fig. 81a, b, incomplete ventral valve viewed ventrally and posteriorly; the left side of the delthyrium and the tooth have been broken, but the thickened dental ridges and low median ridge are clear. BB63460, ×7. Fig. 82a, b, dorsal valve, interior and posterolateral view; the cardinalia are well preserved with paired projecting crura (arrowed) and posteriorly recurved cardinal process. BB63459, ×7.

name is derived from the Lanarkshire town of Carluke, so should be without the 'i' as it first appeared in print (1859: 59); this is the spelling utilized here.

Davidson thought this small rounded species was related to the similar *Crurithyris urei*, but noted that *N. carlukensis* is equally biconvex whilst *C. urei* is strongly ventri-biconvex. Five specimens are attached to the card in the BM(NH) collections with Davidson's handwritten label marked 'Sp. Carlukiensis'. Of these, two are *Crurithyris* species; from the remaining three the lectotype (B7627) has been chosen. It is probably the specimen figured by Davidson (1859: pl. 13, figs 14), but as two specimens are virtually identical it is impossible to be sure. Davidson noted that his species occurred near Carluke in association with the much commoner *C. urei*. This too is true in the silicified Co. Fermanagh faunas.

In 1863 Davidson illustrated (pl. 55, figs 14, 15) more specimens named 'Spirifera carlukiensis', this time from Narrowdale, Staffordshire. These range in width from 7 to 12·5 mm but otherwise bear external similarity to the type specimens. Their shell is partially exfoliated exposing a coarsely fibrous secondary shell structure, the fibres being up to about 0·03 mm wide. This contrasts with the very fine secondary fibres of the Carluke specimens and reinforces the doubt as to these two forms being conspecific; the Narrowdale specimens are possibly young specimens of *Coledium*.

The number of specimens of *N. carlukensis* recovered from the Fermanagh limestone is relatively small, there being about 50 reasonably preserved valves, including valves down to 1·4 mm wide. Even in these smallest valves the dorsal cardinalia are relatively large and neither the shell shape nor the internal morphology altered to any marked extent during ontogeny, other than by size increase. Variation within the assemblage can be recognized in details of the cardinalia, some of which taper distally more rapidly than others, leading to a narrow and almost pointed tip, contrasting with the more normal wide bifid tip. It is to be expected that this characteristic would correlate with the width and length of the delthyrium, into which the exterior surface of the cardinal process fits. Unfortunately, however, there are insufficient associated dorsal and ventral valves to allow direct observation of this feature.

The rarity and small size of these brachiopods probably accounts for their absence from the British literature. *Nucleospira* species have been described from the well-preserved Mississippian shale faunas of North America, and species such as *N. barrisi* White and *N. minima* Weller appear to be very similar to *N. carlukensis*, the latter especially so in size. These species are found in rocks of about mid to upper Tournaisian age. A third species, *N. superata* Easton from the Cameron Creek Formation of Montana, is very similar externally to *N. carlukensis*, but the important characteristics of the cardinalia were not described (Easton 1962). The age of the Cameron Creek Formation is uncertain, but Easton suggests that his *Nucleospira* species is of Chester age, the age commonly accepted for the underlying Heath shales. If this is correct, *N. superata* is slightly younger than *N. carlukensis* from northern Britain. Neither the reviewed European nor Russian literature records *Nucleospira* species and, judged by the published faunal illustrations, the genus would not seem to be present under a different name.

If the paucity of *Nucleospira* species and specimens is genuine, rather than collecting failure, it may be that the present distribution can be explained as that of a migrating group of species, close to the limits of their environment, undergoing allopatric (geographical) speciation; the distribution would be from North America, where the group is well represented in the Devonian, to Britain by mid to upper Viséan time, and becoming confined to northern and central North America by the uppermost Mississippian.

Superfamily **CYRTIACEA** Frederiks 1919 (1924)

Family **AMBOCOELIIDAE** George 1931

Genus ***CRURITHYRIS*** George 1931

Type species. *Spirifer urei* Fleming 1828: 376 (as figured by Ure 1793: pl. 14, fig. 12), by original designation of George 1931: 43. Lectotype selected by George (1931: pl. 4, figs 1a–d), Ure Collection, Hunterian Museum, Glasgow (L1790), from high D zone, Viséan of Strathaven, Lanarkshire, Scotland.

Description. Strongly ventribiconvex Ambocoeliidae with hinge line less than width of shell. Commonly with microspinose external ornamentation. Cardinal process sessile to low with ridged to tuberculate myophore, adductor scars commonly enclosed posteriorly by crural bases and extending anteriorly up to two-thirds of valve length. Dental plates lacking.

Discussion. Additional information about the valve interiors necessitates a revision of the diagnosis. It is suspected that all *Crurithyris* species were originally spinose externally and that it is simply lack of preservation which has led to the reporting of smooth species. A form of spinose ornamentation can often be recognized on well-preserved shale specimens and upon many finely silicified specimens. Material cracked from limestone has commonly lost its external shell because the ornamentation clings to the surrounding rock.

The genus is widely distributed in high Devonian through to low Permian strata. It appears not to have persisted into the Carboniferous of Australia, although known from the upper Devonian of Western Australia. The Givetian species *C. jurkowicensis* Balinski 1973, from the Holy Cross Mountains, Poland, might be placed more appropriately in the genus *Ambocoelia*.

Crurithyris urei (Fleming)

Figs 83, 85–92

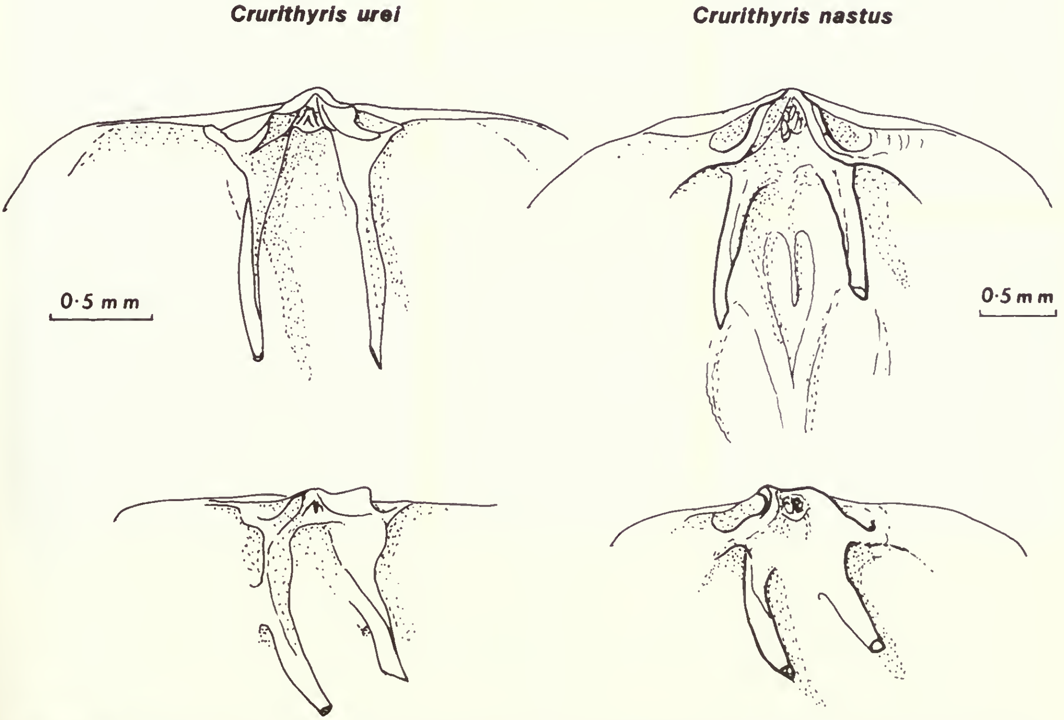
1793 [un-named] Ure: pl. 14, fig. 12.
v* 1828 *Spirifer urei* Fleming: 376; specimen figured by Ure.

1859 *Spirifera urei* (Fleming); Davidson: 58 (*pars*); ? pl. 12, figs 14.
? 1899 *Ambocoelia parva* Weller: 20; pl. 4, figs 1–4.
1931 *Crurithyris urei* (Fleming) George: 55; pl. 4, figs 1–4.
v. 1931 *Crurithyris magnispina* George: 50; pl. 5, figs 1–4.

DIAGNOSIS. Small, anteriorly weakly sulcate *Crurithyris*; exterior with fine growth lines, ornamentation of small and minute spines with or without superficial radial grooves. Dorsal adductor scars anterior to pedicle adjustor scars, placed between widely-spaced subparallel crura. Ventral valve lacking median ridge.

LECTOTYPE. *Spirifer urei* Fleming, Ure Collection, Hunterian Musuem, Glasgow (L1790). Selected by George (1931: 55).

DESCRIPTION. Small ventribiconvex shells with an apsacline ventral interarea and very short catacline dorsal interarea. The dorsal umbo is slight and both valves are weakly sulcate anteriorly. Growth lines are very fine, commonly ill-defined or more clearly developed only anteriorly. The external surface is pitted by minute cavities, arranged more or less concentrically with a frequency of 15 to 20 per mm width, from which extend minute spinose projections in exceptionally well-preserved specimens. A set of larger spinose projections occurs on ventral valves with a spacing of 0·1 to 0·2 mm (Figs 92b, c). Teeth are small, semi-oval in outline and project a little medially of the margin of the delthyrium, which is bordered by narrow deltidial plates and internally by low dental ridges (Figs 88b, c, 89). Ventral muscle scars are lightly impressed, the adductors being confined umbonally and more or less narrowly obovate in outline. The diductor scars appear to be widely spread from the anterolateral margins of the adductors. A ridge of secondary shell bounds the delthyrial apex internally and confines the posterior ends of the muscle scars. Within the dorsal valve the cardinal process is a small



Figs 83–84 Drawings of the dorsal valve interiors of *Crurithyris urei* and *C. nastus*, to illustrate differences in the inner socket ridges and crural bases. The upper two drawings are viewed dorsally, the lower two obliquely.

tuberculate or weakly longitudinally ridged area raised on the short notothyrial platform situated within the apex of the inner socket ridges (Fig. 90b). While the sockets themselves are shallow the inner socket ridges are prominent, especially anteriorly, so as to articulate strongly with the teeth. Crural bases support the sockets and extend dorsomedially to fuse with the valve floor posteriorly. There are no inner hinge plates. The crura are subparallel and extend about two-thirds of the dorsal valve length before curving ventrolaterally (Fig. 90) into the ribbon of the three-coiled spiralia. The posterior pair of adductor scars are slightly sunken, elliptical in outline and extend anteriorly from between the crural bases. The anterior adductor muscle scars are commonly less well defined and flank the posterior scars anterolaterally. Their outline and position is variable but generally they are somewhat reniform, tending to enclose the anterior margins of the posterior scars; they trail posteriorly to the crural bases. The complete adductor field is divided medially by a low ridge. Apically, between the crural bases there are indistinct pedicle adjustor muscle scars.

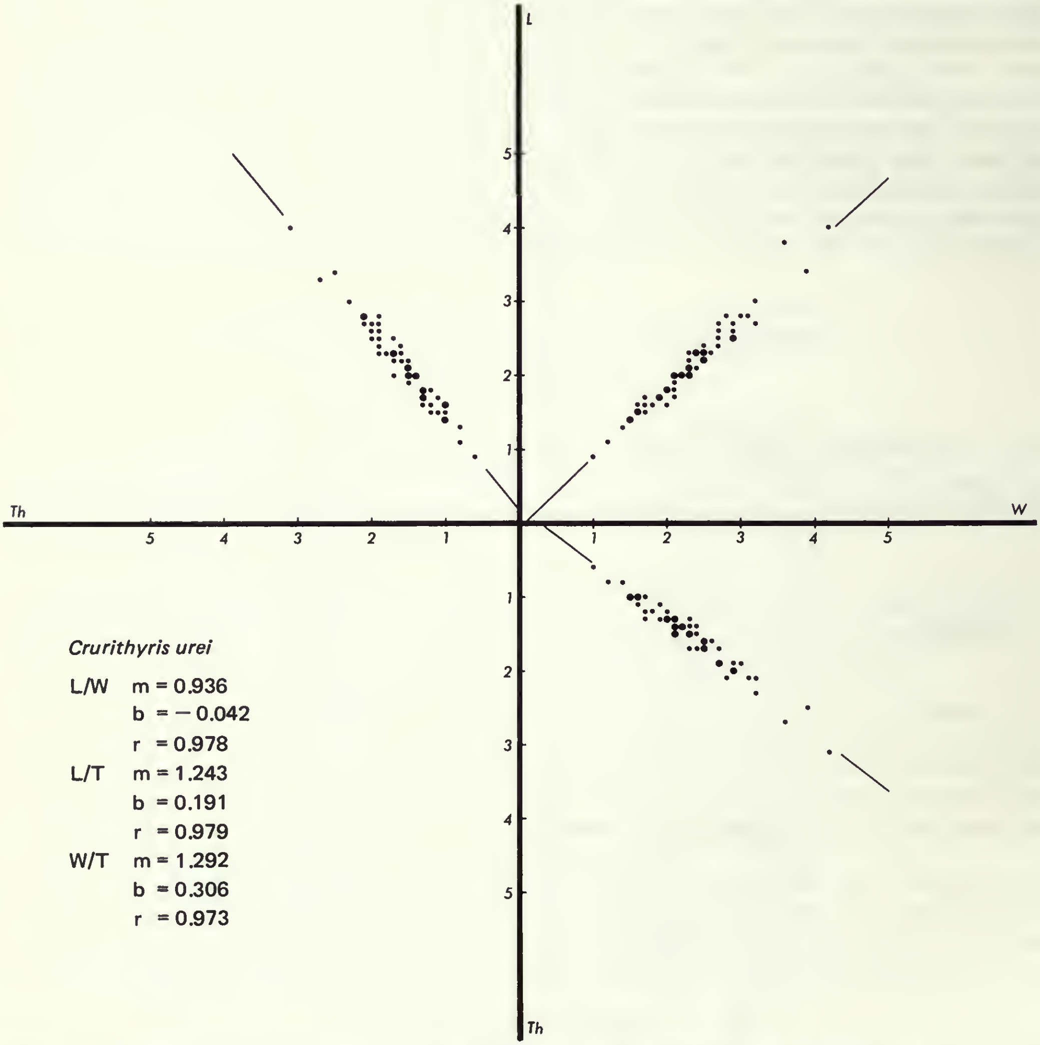
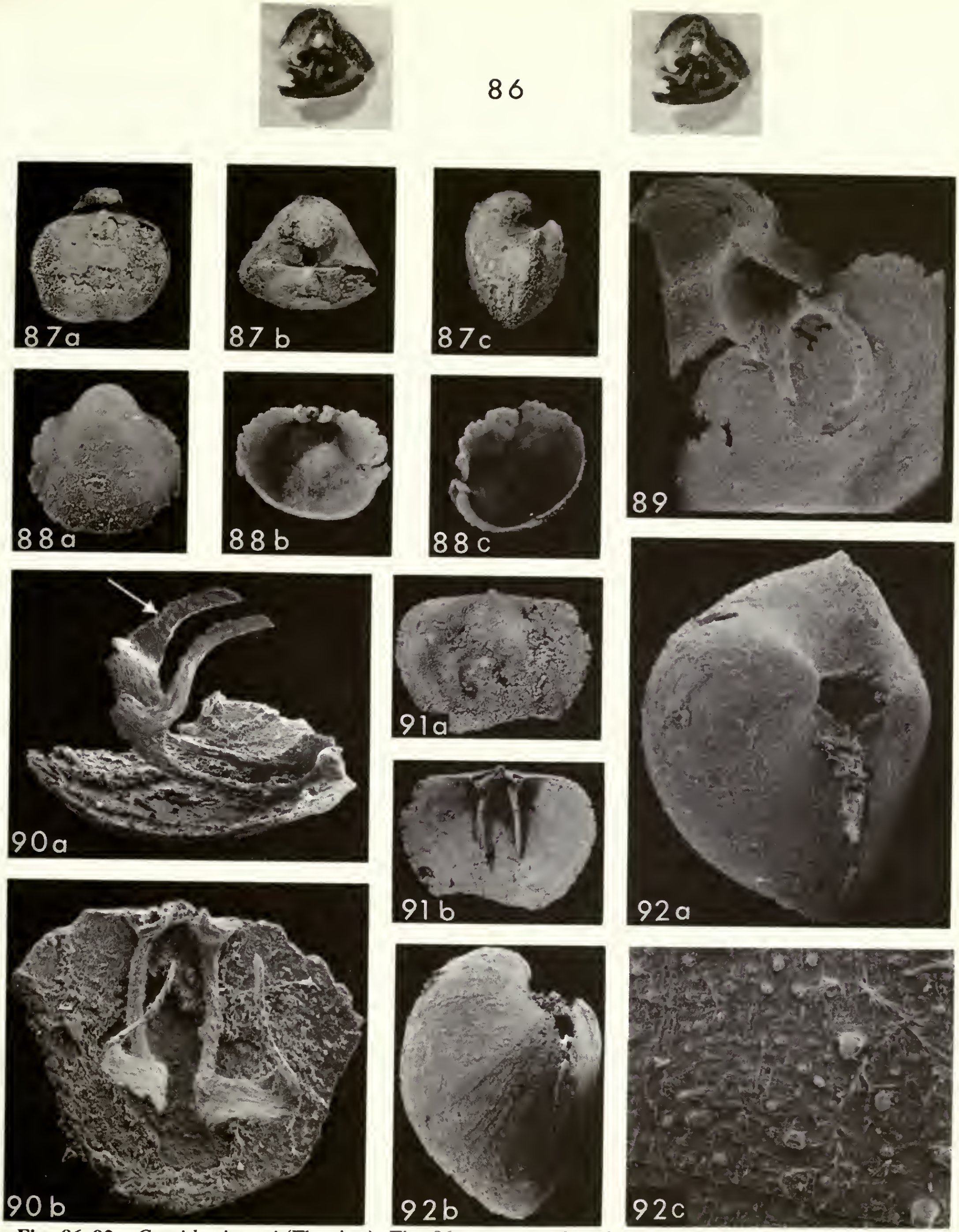


Fig. 85 *Crurithyris urei* (Fleming). Length, width and thickness plots of 60 specimens from Co. Fermanagh. m = slope of regression line; b = intersection point of m with axis; r = coefficient of correlation.



Figs 86–92 *Crurithyris urei* (Fleming). Fig. 86, stereoscopic pair illustrating the interior of a shell, showing the cardinalia and crura. BB63457, ×5. Fig. 87a–c, dorsal, posterior and lateral views of complete adult shell. BB63551, ×5. Fig. 88a–c, external and internal posterior and oblique lateral views of a ventral valve showing the microspinous ornamentation, the teeth and dental ridges. BB63456, ×8. Fig. 89, dorsal valve with articulated ventral valve umbo, viewed internally to show the articulation, dental ridges and crura. BD1170 (broken), S.E.M. ×28. Fig. 90a, b, dorsal valve with complete crura and start of the spiralium viewed laterally and dorsally; note the nodose anterior edge at the start of the spiralium (arrowed) and prominent inner socket ridges. BD150, ×20. Fig. 91a, b, adult dorsal valve exterior and interior. BB63552, ×6. Fig. 92a–c, posterior and lateral views of a complete shell, with detail of the microspinous ornamentation on the anterolateral margin of the ventral valve. BB61624, S.E.M. ×20, ×15 and ×75, respectively.

Discussion. The species is common in the Fermanagh silicified faunas, there being in excess of 500 specimens, but the individuals are small, seldom reaching more than 4 mm in length (Fig. 85). The lectotype is 4·3 mm long and Ure's largest specimen is 4·8 mm long (from George 1931). Like *C. parva* (Weller), as shown by Carter (1967), *C. urei* changed little in its relative dimensions during ontogeny. Curvature of the valves is most marked posteriorly so that the young dorsal valve is relatively more convex than that of adult shells, which like the ventral valve becomes relatively flattened anteriorly.

The spinose external ornamentation is very fine, yet was noted by Davidson in 1859 and illustrated by him in 1863 (pl. 54, fig. 14). George (1931) described this feature in some detail and utilized the presence of two sizes of 'spines' on both valves as a characteristic of his new species *C. magnispina*; he considered all the Davidson (1859, 1863) figures, called *S. urei*, as illustrating his new species. However, George noted that 'in certain forms the larger spines occur only on the anterior and lateral portions of the dorsal valve, the umbonal region being only microspinous'. Thus, only in fully grown specimens of this large species, reaching about 9 mm in length, were the characteristic big 'spines' seen on dorsal valves. On smaller specimens, at sizes characteristic of *C. urei* (3 to 4 mm long) the spinose arrangement would have been as recorded for *C. urei*. The differentiation of these two species included details of the dorsal adductor muscle scars, disposition of crural bases and overall size, features which appear to have varied sufficiently within themselves to allow a continuous gradation and indeed overlap between the two species, which here are considered synonymous.

Crurithyris fissa George, from the D_2 zone 'reefal' limestones of Parkhouse Hill, Derbyshire is distinct whilst *C. amoena* George, from the uppermost Viséan of the Gower, is very similar to, and possibly conspecific with, *C. urei*. A large sample of *Crurithyris nastus* Brunton & Champion 1974, collected by Mr C. Champion in the Manifold valley from rocks probably of early Viséan, Chadian age, superficially resembles *C. urei* but differs in having a distinctly striated cardinal process, less well developed, or posteriorly differentiated, crural bases, and a low median ridge in both valves (see Figs 83, 84).

The spinose external ornamentation is only preserved in some shale specimens and acid-developed silicified material. Both the smaller and larger 'spines' are arranged in ill-defined concentric bands but the larger 'spines' are less regular in their occurrence. All seem to be solid, but as George (1931: 37) suggested, it seems probable that while close to the valve margin these spines were tubular, their inner surfaces being lined with secretory epithelium. The minute cavities marking the positions of abraded spines indicate that the epithelium probably plugged the spine end with calcite and then atrophied. The epithelial evaginations would have been pinched off from the outer mantle epithelium and secondary shell secreted over the inner ends of the cavities, which project slightly into the shell looking a little like a very fine endopunctation, as seen from the valve exterior. On rare specimens small grooves about 0·2 mm in length extend anteriorly from some of the 'spine' bases. These grooves probably represent the refusion of the mantle epithelium, and consequently of the primary shell layer, at the distal (marginal) side of the spine, following the budding of the generative epithelium responsible for the growth of the spine (see Brunton, 1976).

The dorsal musculature for *Crurithyris* presented by George (1931: fig. 3b) is based upon an internal mould of his species *C. amoena* (also figured 1931: pl. 5, fig. 6) and as such is an overgeneralization of the situation. Although it is true that the dorsal muscle field is generally confined within the anteriorly-extended lines of the crural bases, the adductor muscle scars themselves are variably positioned and shaped. It could be argued that the posterior scars are positioned between the crural bases and that the anterior pair of adductor scars is subdivided. Alternatively, and more likely, all the adductor scars are positioned level with or anterior to the anterior ends of the crural bases and the small indistinct scars distinguishable posteriorly, close to the base of the cardinal process, are those of pedicle adjustor muscles. The anteriormost position of adductor muscle scars is about two-thirds of the dorsal valve length (in a valve only 2·6 mm long). This rather more anterior grouping of the adductor muscle scars in *C. urei* places them in an intermediate position between George's (1931) fig. 3 'A' and 'B', 'A' being a representation of the dorsal valve interior of *Ambocoelia*. In separating *Crurithyris* from

Ambocoelia Hall, 1860, George stressed differences in the dorsal musculature and cardinal process. In fully-developed specimens of *A. umbonata* (Conrad), the type species, the cardinal process is weakly striated in much the same way as in some larger *Crurithyris* species. The dorsal musculature of the type species of both genera are more similar than suggested by George and their classification together in his family group Ambocoeliidae is satisfactory. It may be that mid-Devonian *Ambocoelia* species evolved via the Manifold valley *Crurithyris* forms to the high Viséan *C. urei* and *C. fissa*.

Range. *Crurithyris urei* (Fleming) is typical of high Viséan rocks in northern Britain. A similar but distinct species, *C. nastus*, occurs in older rocks probably of low Viséan age in the Derbyshire–Staffordshire area, and the similar species *C. amoena* occurs in high Viséan rocks of south Wales. Well-authenticated occurrences of *C. urei* are lacking from western Europe, but it is recorded from high Viséan and less commonly down to Tournaisian strata of the Moscow basin (Sarycheva & Sokolskaya 1952). Aizenverg (1966, 1971) figures the species from Tournaisian strata in the Donetz Basin, but from the illustrations this record seems doubtful. Neither the species nor any closely comparable have been described from the Viséan of Australia. Weller's (1899) Tournaisian species, *Crurithyris parva* from the south-western U.S.A., is similar to *C. urei*, but is placed in synonymy with considerable doubt!

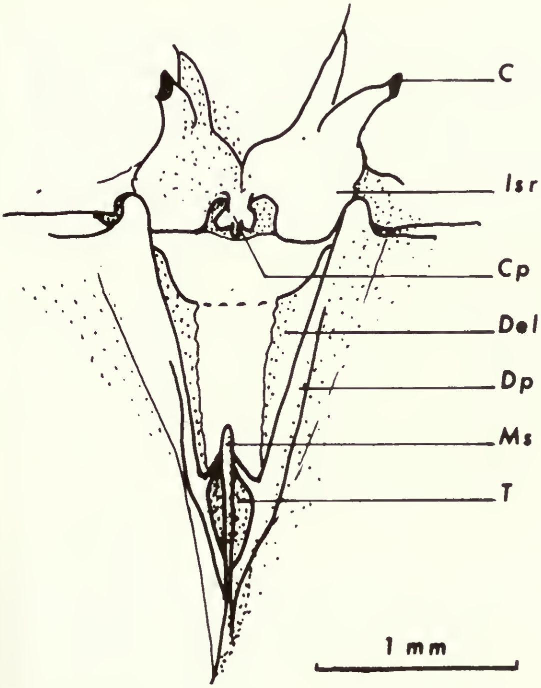


Fig. 93 Drawing of the internal umbonal structures of *Cyrtina hibernica* sp. nov. (see Figs 101, 102). The dorsal valve is uppermost. C = crura; Isr = inner socket ridge, articulating with a tooth laterally; Cp = cardinal process; Del = deltidial plate; in adulthood, these met medially as a complete cover; Dp = dental plate, descending to fuse with the median septum Ms; T = tichorhinum, developed as a pair of chambers, one each side of the median septum.

Superfamily **SUESSIACEA** Waagen 1883

Family **CYRTINIDAE** Frederiks 1912

Genus ***CYRTINA*** Davidson 1859

Type species. *Calceola heteroclita* Defrance 1828: 306, by subsequent designation of Miller (1889: 342) – see Anderson, Boucot & Johnson (1969).

Discussion. The genus was well described by Davidson (1858: 66), Hall & Clarke (1894: 43) and Weller (1914: 286). The type species is from mid-Devonian strata and it was at that time that the genus appears to have been most prolific. The generic name has been used for British Lower

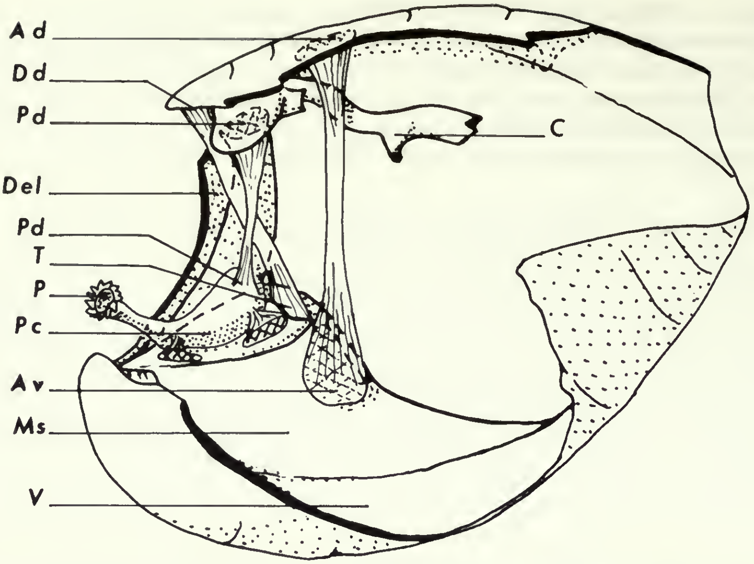


Fig. 94 Diagrammatical reconstruction of the musculature of *Cyrtina hibernica* sp. nov., viewed laterally. C = crura, with the stump of the jugum; Ad = dorsal adductor muscle scar; Dd = dorsal diductor muscle point of attachment, the cardinal process; Pd = dorsal attachment, on the inner socket ridge, of the pedicle adjustor muscle, with its origin from the pedicle capsule, Pc; Del = part of the delthyrial cover; T = tichorhinum, accommodating the ventral ends of the diductor muscles; P = the distal end of the pedicle; Pc = pedicle capsule, from the ventrolateral margin of which extend short adjustor muscles attached to the inner surfaces of the dental plates; Av = ventral attachment area of the adductor muscle; Ms = posteriorly high median septum, accommodating the muscle; V = floor of the ventral valve.

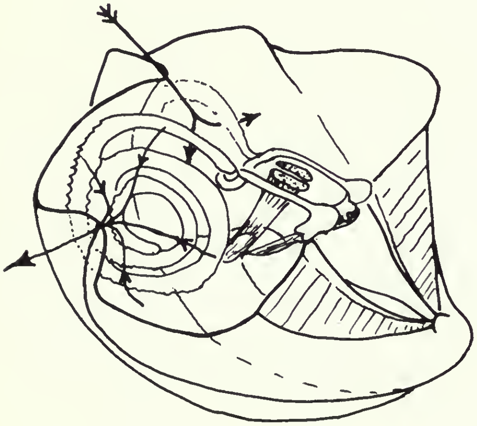


Fig. 95 Diagrammatical reconstruction of *Cyrtina hibernica* sp. nov., showing the inferred feeding/respiratory flow of water through the spiralia. The dorsal valve is drawn as if transparent, to show the left spiralium and the adductor and diductor muscles.

Carboniferous species, such as *C. septosa* (Phillips), *C. dorsata* (M'Coy) and *C. carbonaria* (M'Coy), but these species are now placed in *Davidsonina* Schuchert & Le Vene 1929, leaving no well-known *Cyrtina* species in the Carboniferous. However, Davidson (1863: pl. 52, fig. 15) has illustrated a *Cyrtina* species, which he called *Spiriferina insculpta* (Phillips), from the Lower Scar Limestone of Settle. The whereabouts of this specimen is unknown but within Davidson's unfigured collection in the BM(NH) there are three conspecific specimens from the Wetton district of Staffordshire (B5416), also called *Spiriferina insculpta* by Davidson (ms label). The Fermanagh specimens are the first British Carboniferous *Cyrtina* species to be named, within the modern concept of the genus.

Cyrtina hibernica sp. nov.
Figs 93–107

? 1863 *Spiriferina insculpta* (Phillips); Davidson: pl. 52, fig. 15.
? 1974 *Cyrtina* cf. *burlingtonensis* Rowley; Brunton & Champion: pl. 110, figs 17–19.
1976 *Cyrtina* sp.; Brunton: pl. 115, fig. 7.

DIAGNOSIS. Small *Cyrtina* reaching nearly 8·00 mm wide with three prominent dorsal and four ventral ribs. External ornamentation finely papillose to microspinose. Ventral median septum prominent posterior to tichorhinum, below deltidial plates.

MATERIAL. The species is common from both the collecting localities but most are figured from the Sillees river locality.

HOLOTYPE. BB63704 from the Sillees river locality (Fig. 97).

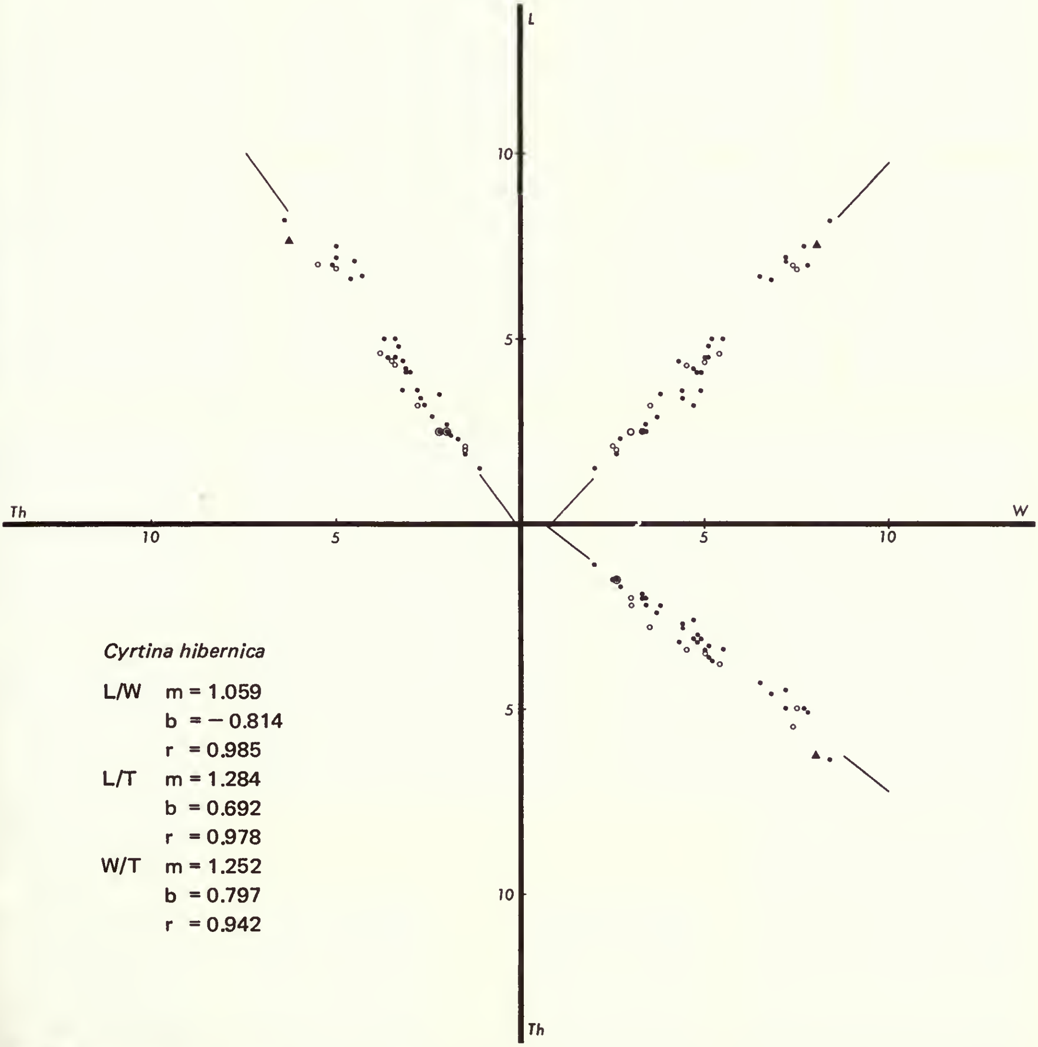
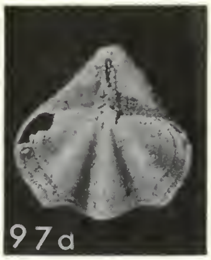


Fig. 96 *Cyrtina hibernica* sp. nov. Length, width and thickness plots of 30 specimens from the Sillees river locality (●) and 10 specimens from the Carrick Lough locality (o); the holotype is differentiated (▲). m = slope of regression line; b = intersection point of m with axis; r = coefficient of correlation.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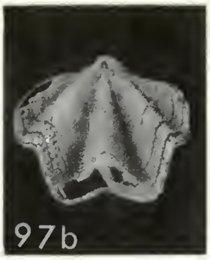
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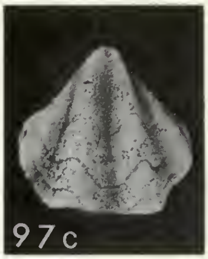
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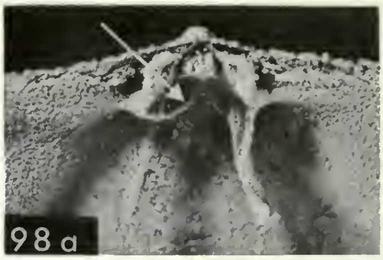
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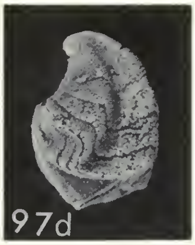
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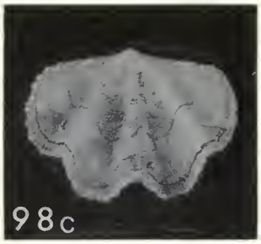
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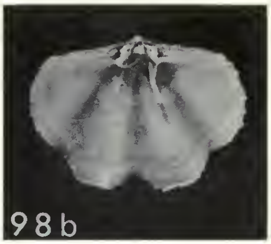
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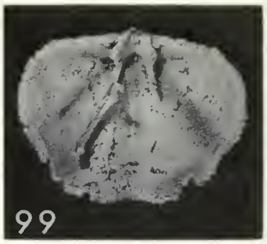
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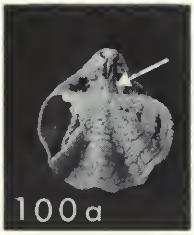
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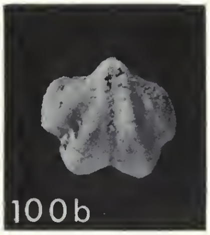
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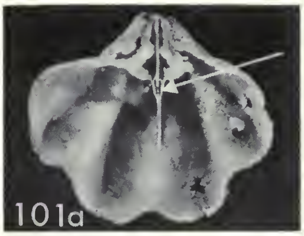
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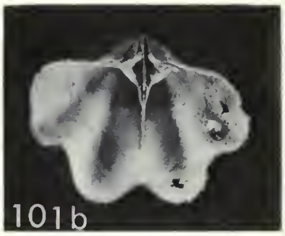
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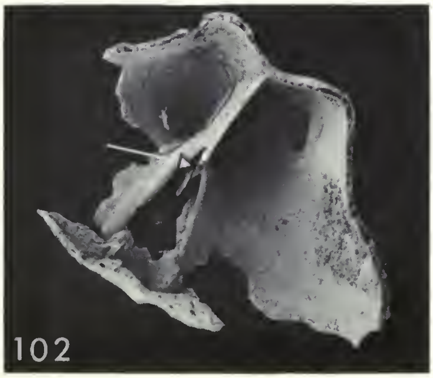
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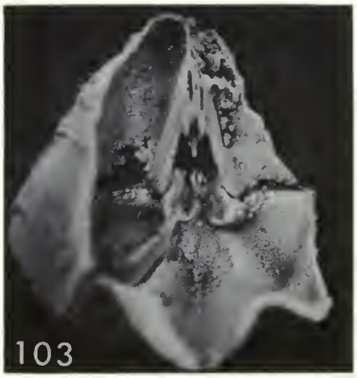
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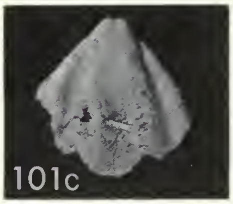
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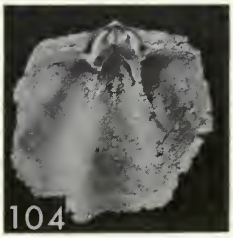
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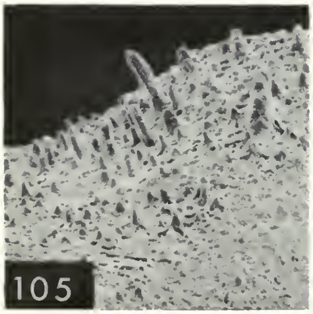
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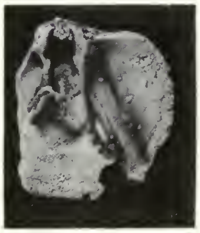

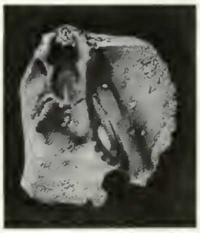

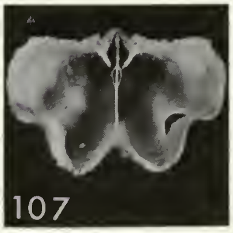
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DESCRIPTION. The outlines of this species are typically cyrtiniform, but in lateral profile the ventral interarea is always apsacline. The external ornamentation is of few prominent ribs, the ventral median sulcus and dorsal median rib originating at the umbones, and the additional pair of ribs on each valve starting within the first 1 mm of growth. Growth lines are developed sporadically and external surfaces are ornamented by minute papillations and true microspines (Fig. 105). The delthyrial covering is variably developed; deltidial plates arch the delthyrium, especially dorsally (Fig. 101), and may fuse leaving a posteroventral narrowly ovate pedicle aperture (Fig. 97a).

The ventral valve has short, rounded, knob-like teeth (Fig. 103) supported by dental ridges which extend ventrally into the dental plates, forming a spondylium-like structure raised high from the floor of the valve by the median septum (Fig. 101b). The posterior edge of the median septum forms a conspicuous plate-like ridge along the 'spondylium' from the umbo to beyond its dorsal extremity. The tichorhinum is divided by the median septum and is supported posteriorly by the dental plates (Figs 101a, 102). The dorsal edge of the median septum is almost perpendicular to its posterior edge within the 'spondylium'. Dorsally concave, arcuate, low ridges on the median septum are growth features, possibly associated with muscle scars. Adult dorsal valve interiors have short, laterally tapering, flat interareas bordering shallow sockets (Fig. 104). The internal socket ridges are high blade-like structures providing the main articulatory surfaces (Figs 99, 103); they diverge from the umbo at approximately 90° from one another, but towards their anterior margins they tend to recurve posterolaterally. The adult cardinal process is normally bilobed with longitudinally striated myophores (Fig. 98a). The bases of the socket ridges, together with the crural bases, form what is almost an anteroventrally-directed concave sessile cardinal plate. The dorsal pedicle adjustor muscles probably attached to this area, at the bases of the crura (Fig. 98a). The crura extend anteriorly, following the positions of the sulci bordering the median rib. At a length of about 0·6 mm a ventroposterior prong from each crus bends anteriorly to fuse medially as a complete jugum (Fig. 106). There is a short, anterodorsally-projecting median process which, together with the jugum, is tuberculate on its anterior surface. The brachial axis is directed slightly posteroventrally of laterally and each spire seems to have had no more than three coils, each of which is strongly fimbriate anteriorly. On the floor of the dorsal valve indistinct low ridges border the adductor muscle scars medially and laterally.

ONTOGENY. From the Sillees river locality the proportions of complete shells to disarticulated valves is about 100 shells to 150 ventral valves and 110 dorsal valves. The total numbers recovered from both localities are about twice these figures. The size range of the specimens is from 1·5 mm wide to 8·0 mm wide (Fig. 96), allowing excellent opportunity for ontogenetic study and a more complete description of internal structures than has been possible hitherto.

Figs 97–107 *Cyrtina hibernica* sp. nov., from Co. Fermanagh. Fig. 97a–d, **holotype** viewed dorsoposteriorly, dorsally, ventro-anteriorly and laterally; note the incomplete delthyrial cover. BB63704, ×3. Fig. 98a–c, a dorsal valve viewed respectively internally, showing details of the cardinalia (crural base arrowed) ×15, and internally complete ×5, and externally ×5. BB63709. Fig. 99, dorsal valve interior with part of the first coil of the spiralia preserved; Carrick Lough locality. BB63823, ×5. Fig. 100a, b, young shell viewed posterodorsally, showing the incomplete delthyrial covering (arrowed), and dorsally; Carrick Lough locality. BB63824, ×3. Fig. 101a–c, a ventral valve viewed posterodorsally and dorsally showing the relationships of the 'spondylium', tichorhinum (arrowed) and deltidial plates (×4), and viewed externally (×3). BB63705. Fig. 102, internal structures (tichorhinum arrowed) of an incomplete but articulated shell. BD109, S.E.M. ×12. Fig. 103, cardinalia and articulation of an incomplete, but articulated, shell. BD107, S.E.M. ×8. Fig. 104, internal view of a mature dorsal valve showing the cardinal process, strong internal socket ridges and large crural bases. BB63708, ×5. Fig. 105, margin of ventral valve showing the external microspinose ornamentation. BB61627, S.E.M. ×50. Fig. 106, stereoscopic pair of photographs of dorsal valve interior showing jugum and first loop of spiralium, with its nodose anterior edge; Carrick Lough locality. BB63822, ×7. Fig. 107, internal (ventral) view of an immature ventral valve; there is a circular bore-hole towards the margin on the right hand side. BB63706, ×5.

Even in the smallest ventral valves the median septum is conspicuous protruding apically into the delthyrial opening. The 'spondylium' and tichorhinum are not developed. At a shell width of 2·00 mm the dental plates are just distinguishable and fuse to the median septum forming a rudimentary tichorhinum. The cardinal process is minute and the jugum arises from the crura at about half the dorsal valve length, i.e. at about 0·8 mm from the dorsal umbo. By a shell width of 3·00 mm the 'spondylium' and tichorhinum are well developed, the former extending to about one-third of the length of the delthyrium, the margins of which are already arched by rudimentary deltidial plates. The cardinal process is a distinct knob-like structure, the inner socket plates are well developed but the position of the jugum is still at nearly half the dorsal valve length. Thereafter growth continued regularly, except that the cardinal process commonly became bilobed by a shell width of 4·00 mm, and the degree of growth of the deltidial plates varied. From the available material it seems that the development of a complete deltidium in adults was unusual. As all stages between well-separated and fused deltidial plates can be observed the term deltidium is appropriate. However, the median line of junction cannot be seen on the deltidium and were it not for the evidence from other specimens this structure would be termed a pseudodeltidium. *Cyrtina* is normally defined as having a pseudodeltidium, but in terms of growth it seems likely that other *Cyrtina* species also possess deltidia developed as in *C. hibernica*.

Within the dorsal valve anterior migration of the jugum (accompanied by resorption along its posterior edge) did not keep pace with the anterior growth of the primary lamella. Thus, by adulthood (valve length of about 4·00 mm) the jugum is only 1·5 mm from the dorsal umbo; it remains at this position during further growth of the shell.

DISCUSSION. The relationship of *C. hibernica* with certain other *Cyrtina* species is reasonably clear. It is most closely related to *C. burlingtonensis* Rowley, originally described from the base of the Burlington Limestone, Missouri, U.S.A. The species has since been described from other formations in the U.S.A. of Kinderhook or low Osage age (= Tournaisian). The two species differ in that *hibernica* always has three dorsal and four ventral ribs, compared to the five and six of *burlingtonensis*; the 'spondylium' is deeper, within which the median septum is higher, and it would seem that the deltidial cover is less well developed in *hibernica*. Brunton & Champion (1974) described two specimens from possible Chadian to early Arundian rocks near Wetton, Staffordshire, as *C.* cf. *burlingtonensis*. These two specimens are very similar to *C. hibernica* and should perhaps be included here. However, the complete specimen from Wetton shows faint additional ribs laterally and so approaches *C. burlingtonensis* in this feature. Considering its stratigraphical position, the Wetton form may be considered as an intermediate. There is a clear trend from the Devonian species, *C. heteroclita*, to this new species in which the ribs are reduced in number and the differentiation of the median fold and sulcus reduced in prominence. The cardinal angles (from the interarae to the ventral valve flank) change from acute to rounded and the delthyrial covering appears to have been reduced during evolution from Devonian through the Lower Carboniferous.

FUNCTIONAL MORPHOLOGY. The unusual structure of the tichorhinum has led to speculation upon the muscle system of *Cyrtina*. Within the dorsal valve the situation is quite clear; diductor muscle attachment to the posteriorly-facing myophores of the cardinal process, and adductors attached medially between the crura and dorsal pedicle adjustor muscles, which attached onto the crural bases (bases of the inner socket ridges; Fig. 93). In the ventral valve it has been agreed generally that the high median septum provided areas of attachment for muscles. In the *Treatise* (Williams *et al.* 1965) Williams & Rowell would have both the diductor and adductor muscles attached to the median septum and the base of the pedicle housed within the tichorhinum. In his study of spiriferide shell structures MacKinnon (1974) recognized myotest on the flanks of the median septum and within the base of the tichorhinum of a Devonian *Cyrtina* species. He interpreted the tichorhinum as accommodating the adductor muscle bases and the diductor muscle attachment as being on the median septum anteriorly. This muscle arrangement is close to that of Recent articulate brachiopods and is that which perhaps provides the most mechanically sound system within shells the shape of *C. hibernica*. The pedicle and pedicle capsule would have been within the delthyrial cavity and covered, to a variable extent, by the deltidial plates. The ventral pedicle adjustor muscles were probably attached within the 'spondylium', on either side of the median ridge, and the dorsal adjustors to the bases of the inner socket ridges (Fig. 94). Such an arrangement poses the problem that the adductor and diductor muscles must have crossed one another, close to the anterodorsal margin of the median septum, all very close to the median plane of the shell. In order to overcome this problem the muscles must have been very narrow and tendinous. An alternative arrangement, less analogous to Recent brachiopods, is for the adductor muscles to have been attached to the median septum below the tichorhinum, and for the diductor muscles to have been seated in the tichorhinum. In this situation the dental plate–median septum structure would have been a true spondylium in that it would have accommodated the adductor and diductor muscle bases, the former being separated from the latter by the tichorhinum (Figs 93, 94).

RANGE. *C. hibernica* is a common fossil from the sampled rocks at the Sillees river and Carrick Lough localities. It has been found also at a point about one mile NNW of the Sillees locality, on the Milltown Bridge stream, in *Schellwienella*-rich argillaceous limestone of the Glencar Formation. This position would suggest an age slightly older than the main fauna under description. If the Manifold valley *Cyrtina* specimens are conspecific then the species may have its origin low in the Viséan. In western Europe *Cyrtina* species appear to be uncommon but forms intermediate in external characteristics between *C. heteroclita* and *C. hibernica* are known from the Tournai region of Belgium. Closely similar species are not recorded from Lower Carboniferous rocks of Russia. A single specimen of a similar, but relatively wider, species has been recorded from the Utting Calcarenite (mid-Viséan) of the Bonaparte Gulf Basin, Australia (Roberts 1971).

Superfamily **SPIRIFERACEA** King 1846

Family **DELTHYRIDIDAE** Waagen 1883

Subfamily **TYLOTHYRIDINAE** Carter 1972

Carter (1972) proposed this subfamily for 'lamellose Delthyrididae with variable outline and moderately numerous lateral costae; micro-ornament apparently lacking; interior of pedicle valve with high median septum and dental adminicula; brachial valve lacking tabellae'. Besides *Tylothyris* North, he included *Texathyris* Carter 1972, a low to mid-Tournaisian genus from Texas. At family level Carter distinguished the Delthyrididae from the Mucrospiriferidae principally on the presence of a ventral median septum in the former, a characteristic carried through to the subfamily and genus *Tylothyris*. The Tylothyridinae was differentiated from the family group by its lack of the fimbriate micro-ornament typical of Delthyrididae.

Genus ***TYLOTHYRIS*** North 1920

TYPE SPECIES. *Spirifer laminosa* M'Coy 1841, by original designation of North (1920), from Hook Head, Co. Wexford, Ireland.

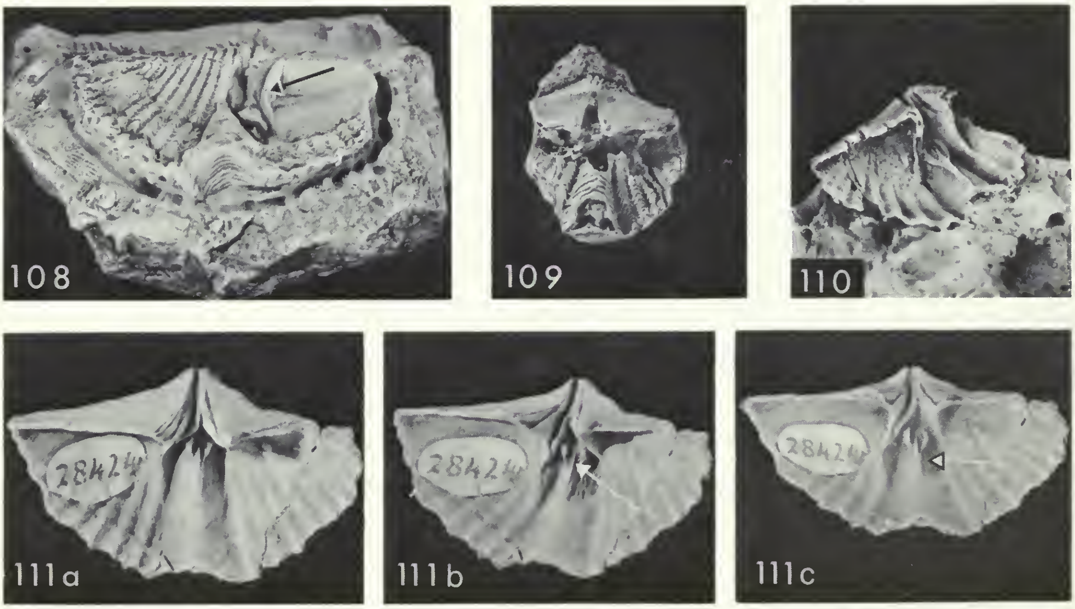
Tylothyris laminosa (M'Coy)
Figs 108–119

1841 *Spirifer laminosa* M'Coy: 26.
1844 *Cyrtia laminosa* (M'Coy) M'Coy: 137; pl. 21, fig. 4.
1858 *Spirifera laminosa* (M'Coy); Davidson: 36 (*pars*); pl. 7, figs 17–20.
1887 *Spirifera laminosa* (M'Coy); de Koninck: 103 (*pars*); pl. 22, figs 44–50; pl. 30, figs 30, 31.
v* 1920 *Tylothyris laminosa* (M'Coy) North: 197; pl. 13, fig. 16.
1920 *Tylothyris laminosa*, mut. γ North: 200; pl. 13, figs 1, 2, 12, 13.

DIAGNOSIS. Transverse *Tylothyris* with concave long ventral interarea and delthyrial angle commonly about 35°; externally convex incomplete delthyrial cover. Nine or ten simple costae on either side of prominent fold and sulcus; entire, regular lamellose growth lines. Dental plates recurved posteriorly to floor of valve and buried posteriorly in apical callosity. Small, raised, narrowly ovate adductor scars separated by low median septum extending nearly half valve length.

Neotype. Contrary to previous designations, M'Coy's species dates from 1841 when, in a descriptive appendix to his catalogue of the Museum of the Geological Society of Dublin, he described the species in the same way as in his better known 'Synopsis' of 1844. There was no figure in 1841, but M'Coy did state that the species was found at 'Hook' (Hook Head, Co. Wexford). The collections of the Society were handed over to Trinity College, Dublin, in 1848, but unfortunately searches there have failed to discover any *Cyrtia laminosa* specimens from the Geological Society, so no lectotype can be selected.

In his redescription of the species North (1920: 198) designated as 'Holotype' a dorsal valve from Hook Head, Co. Wexford, housed in the British Geological Survey, Leeds (IGS 28425; Fig. 108). There is no evidence that this specimen was ever in M'Coy's possession, or in the collection of Griffith, which formed the basis of M'Coy's 1844 'Synopsis', when he repeated his 1841 description. There are eight known Griffith Collection specimens in the National Museum of Ireland, Dublin, labelled as '*Cyrtina laminosa* M'Coy'; they are from Ballinacourty, Co. Waterford, Poulscadden, Co. Dublin (3), Malahide, Co. Dublin (Fig. 109), Ballintrillick, Co. Leitrim (but the village is now in Co. Sligo), and Abbeybeg and Finner, Co. Donegal. None are from Hook Head; the only known Griffith specimens from Hook Head are those in the Sedgwick Museum, Cambridge (E7273 and E7274), both dorsal valve exteriors, and neither of these closely resembles M'Coy's figures (1844: pl. 21).



Figs 108–111 *Tylothyris laminosa* (M'Coy). Fig. 108, the **neotype** selected herein, from Hook Head, Co. Wexford; the dorsal valve has been removed on the right-hand side exposing the dental plates (arrow). Leeds IGS 28425, ×1. Fig. 109, incomplete specimen in the Griffith Collection, National Museum of Ireland, Dublin, from Malahide, Co. Dublin, ×1. Fig. 110, incomplete silicified ventral valve, partially etched from the rock, from Hook Head, Co. Wexford; the internal pitted area, lateral to the thickened dental plates, can be seen. BB56634, ×1·5. Fig. 111a–c, ventral valve interior viewed ventrally, ventrolaterally and ventroposteriorly to show the dispositions of the dental plates, low median septum and raised adductor muscle scars (arrow on Fig. 111b); the diductor muscle scars are arrowed on Fig. 111c. Hook Head, Co. Wexford; IGS 28424, ×1·5.

From M'Coy (1841) and Griffith (1862) it is clear that Hook Head should be the type locality for the species. As no extant Griffith specimen was clearly that figured by M'Coy in 1844, North's specimen (IGS 28425) is here selected as **neotype.**

It is noteworthy that the Griffith Collection was, in all probability, collected by Patrick Ganly, the man responsible for much of the field work leading to the various Richard Griffith geological maps of Ireland published from 1838 (see Archer, 1980).

MATERIAL. Ten Griffith Collection specimens mentioned above, plus one from the Bundoran, Co. Donegal in the Sedgwick Museum (E7272), referred to by North as on tablet 636 (1920: 195). Specimens from other collections include two in the I.G.S., Leeds, and about twenty in the BM(NH), all from Hook Head. From the Fermanagh faunas about thirty reasonably complete shells or valves were recovered, mainly from the Sillees River locality (BB63600–BB63609).

DESCRIPTION. North (1920) provides details of the external morphology and some information about the ventral valve interior. From my observations of topotypic material from Hook Head in the BM(NH) collections, and from the silicified Fermanagh specimens, I disagree with North's description on only a few points. North states that the lateral slopes of both valves are ornamented by ten or twelve costae; my experience is that ten is the common number on adult shells and only on one specimen have I counted twelve. Within the ventral valve the median septum is said to reach nearly to the level of the area at the apex (1920: 196). In young ventral valves (about 8 mm wide) this is not true (Fig. 115) and in older valves the shell thickening buried the median septum apically (Figs 111, 116). In old specimens shell thickening fills the apex of the delthyrial cavity to a level just below the interarea. The median septum extends anteriorly from this callosity well below the level of the interarea, separates the narrowly ovate adductor scars, confined laterally by the thickened bases of the dental plates, and continues anteriorly for about half the valve length (measured parallel to the commissure).

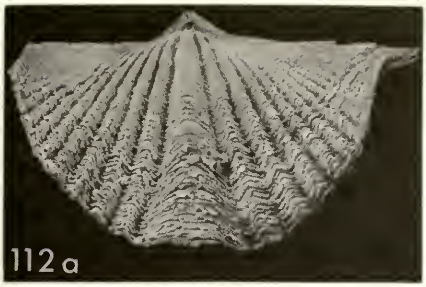
The present silicified material provides information on the internal morphology in addition to that presented by North. The ventral adductor scars are raised on small platforms, the surfaces of which are parallel to the commissural plane (Fig. 111b). As a result of shell thickening only the anterior edges of these muscle platforms remain raised above the valve floor in old age. The diductor muscle scars are indistinct but occupy the flanks of the ventral valve median sulcus and extend slightly beyond the anterior end of the median septum, this is a little over half the total valve length. The disposition of the dental plates differs slightly in the Fermanagh specimens from the Hook Head specimens seen. In the former the anterior edges of the dental plates are strongly concave and do not fully support the anterior edges of the delthyrial margins (Fig. 115). In the Hook Head specimens the dental plates are more fully developed anteriorly, supporting the teeth (Fig. 110). On the lateral flanks of the dental plates, and extending laterally for about half the valve width, the internal surface of the valve is ornamented by a series of shallow pits and irregular ridges (Fig. 118). These areas would appear to be those occupied by the gonocoels within the mantle epithelium.

Dorsal valve interiors have not been described previously. The cardinal process is a wide (reaching 2 mm wide in the largest specimens) comblike structure, having deep longitudinal straight grooves (Fig. 114). In detail each ridge is itself ridged so that the ventral face of the myophore, adjacent to the dorsal umbo, has a rough fimbriate appearance. The cardinal process is separated laterally from the inner socket ridges by a shallow groove and is supported dorsally by a median thickened ridge of shell. This ridge narrows on the floor of the valve to divide the ovate adductor muscle scars, which are situated within the depression of the dorsal fold or fastigium (term of Cooper & Grant, 1976). Low ridges of secondary shell surround the muscle scars posterolaterally and, perhaps, provided the sites of attachment for the dorsal adjustor muscles, close to the base of the cardinal process. The sockets originate about ½ mm apart at the dorsal umbo, and extend anterolaterally across the dorsal interarea at about 55° from the mid-line. They are shallow and their floors buttress out from the inner surface of the valve, dorsal of the interarea (Fig. 114). The inner socket ridges are prominent anteriorly, forming a tight fit with the anteromedian faces of the teeth, and merge anteromedially into the crural bases, which overhang the valve floor about 5 mm apart in the biggest specimens (about 36 mm wide). Neither the jugum nor complete spiralia can be seen in any shell.

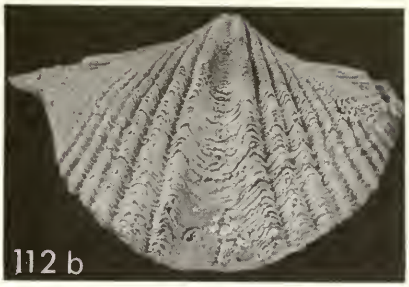
ONTOGENY. The smallest ventral valve (4 mm wide) and dorsal valve (7 mm wide) available already show all the internal structures of adulthood. However, in the ventral valve the dental plates are only 0·3 mm long within the umbo (Fig. 113c) and the delthyrial angle is about 30°, as compared to a maximum of 45° in adult valves. The rate of increase in the delthyrial angle reduced during ontogeny, as compared with the total width of the ventral valve. During ontogeny the number of external ribs increased by additions posterolaterally, up to a total on either side of the mid-line of eleven or, exceptionally, twelve. The sulcus originated at the umbo and its anterior width remained about one-quarter of the total width of the shell. The teeth and sockets grew without shell resorption (deltidiodont of Jaanusson 1971) and the ventral adductor scars became increasingly bounded posterolaterally by secondary shell deposits. Some of the largest valves are thickened marginally, indicating a continuation of shell deposition despite no further growth in overall size.

DISCUSSION. A delthyrial covering has not been described previously for *Tylothyris*, although North was astute enough to recognize that the grooves bordering the delthyrium indicated the likely presence of a covering structure in life (Fig. 113b). In adulthood the delthyrium is partially closed by an apical shell callosity and a small delthyrial plate. Dorsal to the plate is a series of 3 to 4 triangular stegidial plates, the apical points of which imbricate internally with the previously-formed plate. The dorsolateral margin of the stegidial plates fits onto the groove formed between the edges of the delthyrium and shell thickening on the internal sides of the dental plates (Fig. 112e, f). Similar-looking plates are illustrated in *Gypsospirifer* species, from the Permian of southwest Texas, by Cooper & Grant (1976). What is probably a complete stigidium is preserved on only one specimen (Fig. 112), where a narrow gap remains between its dorsal edge and the cardinal process of the dorsal valve. It seems unlikely that the gap accommodated a pedicle in life since the dorsal ends of the diductor muscles must have occupied part of the space and when the shell was open, for feeding etc., the dorsal valve would have rotated towards the gap. Furthermore, there are no clear signs of adjustor muscle scars on the inner surfaces of the dental plates. It is probable, therefore, that the young were attached by a pedicle but that this atrophied towards adulthood, as the stegidium developed, leaving the adult shell with its posterior surface on, or slightly in, the substrate. A feature which may have aided the stability of these adult shells, but which is seldom preserved intact, is the development along the posterior edge of the valves, at the angles with the interarea, of spinose shelly flanges (Fig. 112a). These grew during life as a result of mantle regression leaving the narrowly pointed ears of the ventral valve as projections extending laterally from the sloping 'shoulders' of the valve. Nalivkin (1976) mentions spines in his essay on the form and function of the interarea in spiriferides, which seem to be the same structures. He, however, interpreted the interarea, and these spinose extensions, as resulting from an external generative epithelium from which byssal

Figs 112–119 *Tylothyris laminosa* (M'Coy) from Co. Fermanagh. Fig. 112a–e, complete specimen viewed dorsally, ventrally, anteriorly, laterally and posteriorly. BB63610, ×1·5. Fig. 112f, same specimen showing stegidial plates. BB63610, ×3. Fig. 113a–c, juvenile ventral valve viewed externally, posteriorly and internally; the juvenile dental plates are arrowed. BB63617, ×4. Fig. 114, interior of adult dorsal valve showing the striated cardinal process (arrowed) and strong inner socket ridges. BB63611, ×1·5. Fig. 115, interior of young incomplete ventral valve, showing dental plates and low median septum (arrowed). BB63616, ×4. Fig. 116, interior of adult ventral valve, showing the lateral deflection of the ridges extending forward from the dental plates and slightly raised adductor muscle scars (arrowed). BB63613, ×1·5. Fig. 117a, b, incomplete young dorsal valve viewed externally and internally. BB63615, ×4. Fig. 118, internal view of incompletely silicified ventral valve, showing the adductor muscle scars medially, parts of the dental plates and parts of the pitted areas of the internal surface. BB63600, ×1·5. Fig. 119a–c, dorsal, ventral and posterior views of juvenile shell; note the asymmetrical growth of the ears and on Fig. 119c the grooves near the edges of the delthyrium. BB63612, ×4.



112 a



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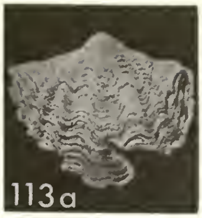

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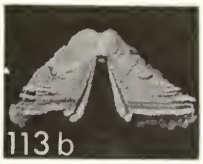

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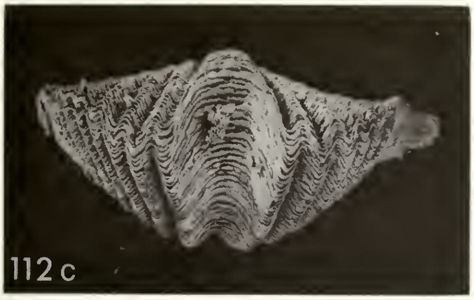

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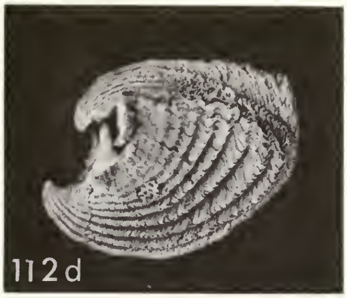

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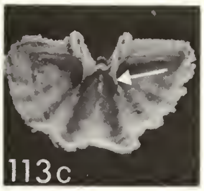

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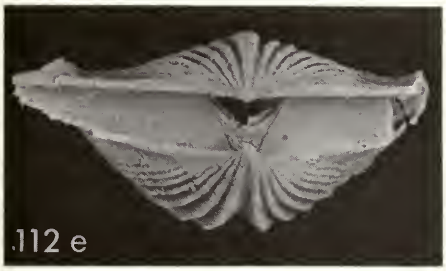

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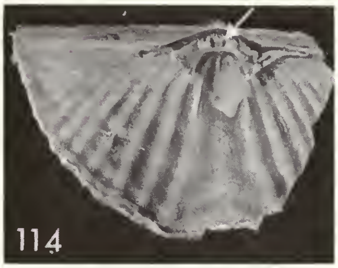

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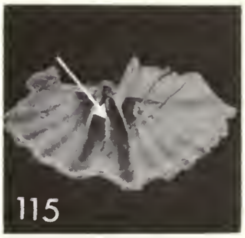

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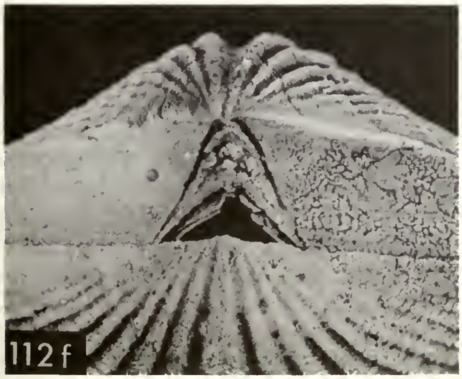
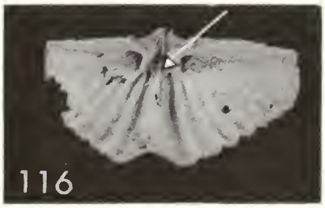


112 f



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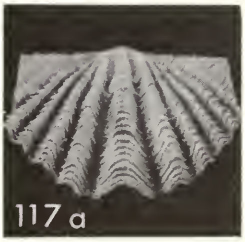

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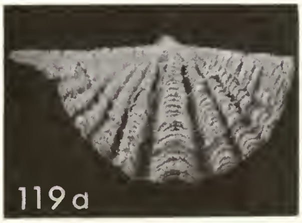

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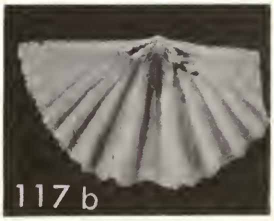
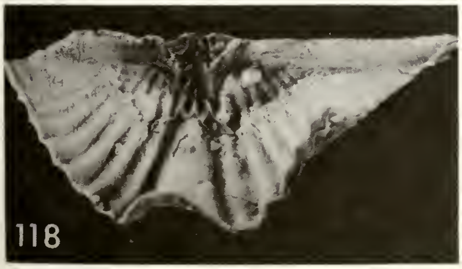


117 b



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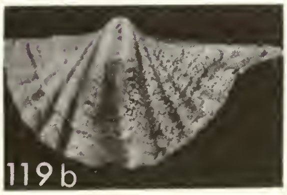
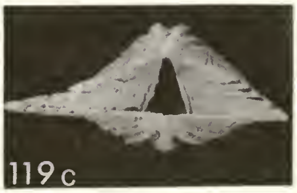


119 b



119 c

filaments grew, attaching the shell to the substrate. I find his argument for a byssal brush covering the interarea unconvincing, and he ignores the important geometrical constraints imposed on the shell growth by the straight, wide hinge line. The fine reticulate pattern of growth lines and perpendicular striations possibly results from unusually thickened periostracal material, developed at the valve margin, leaving growth traces across the interarea. Medially, this periostracal covering would have protected the delthyrial opening and dorsal ends of the diductor muscles. Elsewhere along the hinge line it would have sealed the posterior commissure and, perhaps, aided in the holding of the valves together. Sufficient elasticity would have been necessary to allow hinge movement, and the periostracum on the interareas may have assisted this movement.

The shell articulation is such that the valves would not have held together for long after death of the animal and decay of the articulatory muscles. Only four shells remain articulated and as two of these are young it may be that the population was killed, perhaps by the arrival of unusual quantities of fine sediment. Of the disarticulated valves many show signs of having been broken prior to silicification, and are infested by organisms such as tubiculous worms, fenestrate bryozoan holdfasts or the microscopic ramifications of ctenostomatous bryozoans (Brunton 1966*b*) or phoronids. These features indicate that some dead shells remained on or close to the substrate surface for an appreciable length of time before becoming deeply buried.

RANGE. The species is well known in Belgium, where fine silicified specimens have been collected from the late Tournaisian shales in the Tournai region. Some of these specimens match those from Fermanagh very closely in size and external features. One difference, however, is that the Belgian specimens tend to have more strongly developed, higher, fastigia (term of Cooper & Grant, 1976, for the median dorsal crest), creating well-differentiated folds of the anterior margins, while the dorsal fastigia of Fermanagh shells do not rise much above the bordering ribs. Unfortunately, material from Hook Head, the type locality, is crushed and detailed development of the fastigium and sulcus cannot be observed. Ventral valve interiors, available from Hook Head, Belgium and Fermanagh, show that the development of shell thickening in the ventral umbo, around the dental plates, ventral muscle scars and median septum, varies during late ontogenetic stages to such an extent that comparisons are of little value without the benefit of large collections. Specimens from all three localities seem to have become equally thickened late in their lives, but those from Hook Head and Fermanagh retained a prominent median septum which extends well beyond the dental plates and muscle scars, to nearly half the valve length (Figs 111, 116). However, it is seldom well preserved.

Carter (1967) described *T. brevaurita* from late Tournaisian rocks of central Texas, and compared the species to others from the Mississippian of North America. None of these closely resembles *T. laminosa* although *T. brevaurita* retains a distinct ventral median septum.

Two species of *Tylothyris* have been described from Australia which resemble *T. laminosa*. Firstly *T. planimedia* Cvancara (1958), originally described from New South Wales in rocks thought to be late Tournaisian in age, is now, according to Roberts (1975 and personal communication) considered as Viséan, equivalent to the British D_1, Asbian stage. Gaetani (1968) recognized this species in rocks of the central Elburz, Iran, which appear to be of a late Tournaisian age. The second species is *T. transversa* Roberts, 1971, from the Enga Sandstone (late K zone, Tournaisian) of north-west Australia. Roberts' species differs from *T. laminosa* in having a lower ventral interarea, resulting in the umbones remaining narrowly separated and in the delthyrial angle being 50°–55°, as compared to the 35°–40° in *T. laminosa* from Hook Head. The fold (fastigium of Cooper & Grant, 1976) and sulcus are narrower than in *T. laminosa*, while those of *T. planimedia* have flat bases, with the hint of a faint median rib. Details of the delthyrium, apical callosity and ventral median septum are commonly considered as providing distinctive features. However, in the silicified Fermanagh fauna these features are variable. The delthyrial angle increased with age, the apical callosity increased and the median septum became increasingly buried by the deposition of secondary shell in the ventral valve umbo. For these reasons I do not feel that the distinctions made between the two Australian species, using these features, are meaningful.

Geographically *Tylothyris* species similar to *T. laminosa* extend from western Europe, through the Middle East to Australia. North American *Tylothyris* species are less closely related to *T. laminosa*. Recently Jin & Fang (1983) used the species name for early Carboniferous specimens they described from Yunnan, China, but appear to have ignored its designation as type species of *Tylothyris* by assigning it to *Spinocyrtia* Frederiks, a genus typical of the Devonian.

Stratigraphically, *T. laminosa* is known from the late Tournaisian, in the type locality and in Belgium, and from mid-Viséan rocks in north-west Ireland, including the present Fermanagh fauna. This long range is unusual for brachiopod species, but some are known with equally long or longer ranges. Perhaps significantly, another Hook Head species, *Brochocarina wexfordensis* (Smyth), also occurs in Fermanagh as has been described (Brunton 1968).

When first describing *Tylothyris* North included *T. subconica* (Martin 1809), divided as two subspecies, *subconica* (Martin) and *castletonensis* North, 1920, from D Zone (Asbian and Brigantian) rocks of northern England and of Ireland. These are distinctive shells with high, almost flat, ventral interareas, giving an outline reminiscent of *Syringothyris* or *Pseudosyrinx*.

Family **PAECKELMANELLIDAE** Ivanova 1972

Subfamily **STROPHOPLEURINAE** Carter 1974

Diagnosis (emended). Small to medium transverse Paeckelmanellidae with simple lateral costae ornamented by lirae and commonly with strongly developed growth lines. Fold and sulcus commonly non-costate, with or without median rib and groove; sulcus bounding ribs commonly accentuated, as are corresponding dorsal grooves. Ventral interarea large and denticulate. Dental plates short or heavily thickened. Dorsal sockets small and closely set, cardinal process commonly supported medially by short ridge; shell substance impunctate.

Discussion. While preparing his 1974 paper, Carter was apparently unaware of Ivanova's (1972) classification of spiriferids. In this general study Ivanova erected the new family Paeckelmanellidae, within the superfamily Syringothyridacea. In 1981 Ivanova took the matter a stage further in elevating her 1972 new family to superfamily level – the Paeckelmanellacea. Her familial taxonomy (Ivanova 1981) retained the family Paeckelmanellidae, within which she placed three subfamilies, the Strophopleurinae Carter, the Pterospiriferinae Waterhouse, and the Paeckelmanellinae Ivanova. Within Carter's (1974) subfamily she placed *Strophopleura* Stainbrook, *Acuminothyris* Roberts, *Fusella* M'Coy and *Voiseyella* Roberts. Carter (1974) did not include *Fusella* in his classification, but several of the genera he did include within the Strophopleurinae have been assigned by Ivanova (1981) to her Paeckelmanellinae or to Waterhouse's Pterospiriferinae. While I find it unfortunate that a family, or superfamily, should have been based on an imperfectly known genus like *Paeckelmanella* Lickharev, I agree with Ivanova's concept of a family for the genera she has included in the Paeckelmanellidae.

Brunton & Rissoné (1976) utilized the subfamily Strophopleurinae in their redescription of the genus *Fusella* M'Coy, but erred in assigning it to the family Mucrospiriferidae. The familial diagnostic importance of a denticulate hinge line was stressed by Carter (1974) and Ivanova (1981), and is helpful in distinguishing between members of this family and the Mucrospiriferidae.

Genus ***FUSELLA*** M'Coy 1844

Type species. *Spirifer fusiformis* Phillips, 1836: 210; pl. 9, figs 10, 11, by original designation of M'Coy (1844: 132).

Diagnosis. Small (commonly less than 30 mm wide) to medium-sized, but strongly transverse, fusiform shells, with subcircular lateral profile. Ventral interarea wide, concave and denticulate. Costate ribbing, ill-defined on fold and sulcus, but prominent bordering sulcus. Dental plates close, subparallel and within sulcus.

DISCUSSION. The genus formed the subject of papers by Brunton & Rissone (1976) and Waterhouse (1970). Because the single specimen of *F. fusiformis* described by Phillips is poorly preserved and the species is rare, there being only one other specimen known to me (Davidson Collection specimen B7379 from Dovedale, Derbyshire), both species and genus have remained ill-defined and the genus name has been used incorrectly, especially in some Russian literature. Both specimens of *F. fusiformis* were described and figured by Brunton & Rissoné (1976), who, following Brunton & Champion 1974, suggested that *Spirifer rhomboidea* Phillips belonged to the genus and described its internal structures, as a guide to those of *Fusella*. *Fusella rhomboidea* is a rare member of the Fermanagh silicified faunas.

Fusella rhomboidea (Phillips)
Figs 120–127

v* 1836 *Spirifera rhomboidea* Phillips: 217; pl. 9, figs 8, 9.
1858 *Spirifera convoluta* var. *rhomboidea* Phillips; Davidson: 35; pl. 5, figs 2–8.
v 1974 *Fusella rhomboidea* (Phillips) Brunton & Champion: pl. 111, figs 6, 7.
1976 *Fusella rhomboidea* (Phillips); Brunton & Rissoné: pl. 1, figs 13–17.

DIAGNOSIS. Relatively large *Fusella* about twice as wide as long, with prominent fold, sulcus and costae. Single low dorsomedian costa; first pair of ribs bordering fold bifurcate close to umbo. Ventral interarea denticulate, high and strongly concave. Teeth supported by dental ridges and plates diverging slightly anteriorly and onto valve floor, on flanks of ventral sulcus.

LECTOTYPE. *Spirifer rhomboidea* Phillips, figured 1836: pl. 9, fig. 8; from Bolland, Yorkshire. Gilbertson Collection, BM(NH), B236. Lectotype selected by Brunton & Rissoné, 1976 (Fig. 120).

DESCRIPTION. Fusiform shells throughout ontogeny with a length about half the total width and a little greater than the thickness. On each side there are up to twelve ribs which diminish in size laterally. A low median costa may be developed on the dorsal fold, and the first pair of costae bordering the fold bifurcate within 2 mm of the umbo. Similarly, the pair of costae bordering the

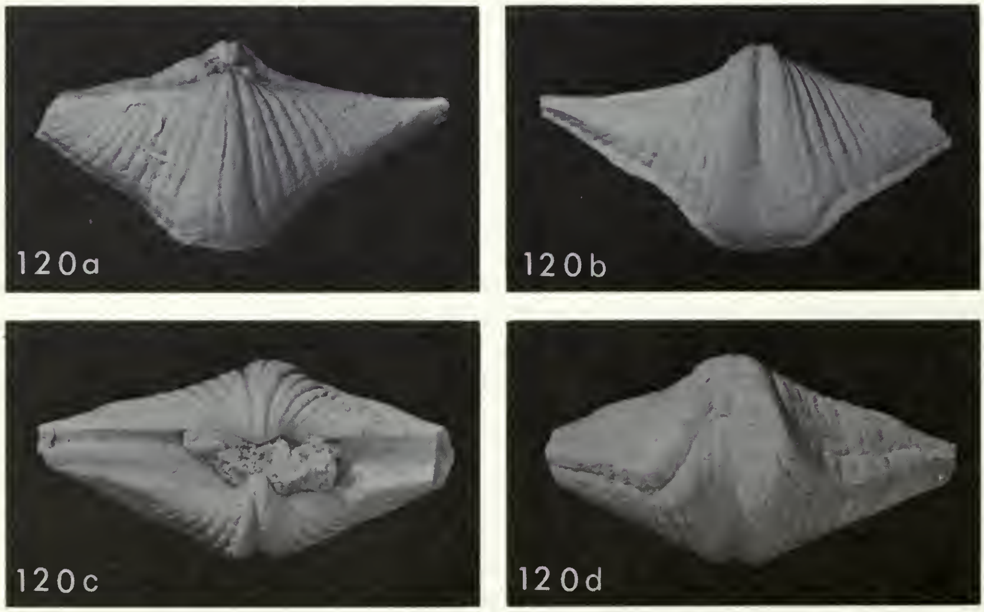


Fig. 120 *Fusella rhomboidea* (Phillips). The lectotype, selected Brunton & Rissoné (1976), from the Viséan of Bolland, Yorkshire, viewed (a) dorsally, (b) ventrally, (c) posteriorly and (d) anteriorly; the shell is stripped from the ventral interarea so the denticulation does not show. B236, ×2.

ventral sulcus may bifurcate laterally, close to the umbo, and a little later in ontogeny a median branching may occur so as to give a pair of weak costellae within the sulcus.

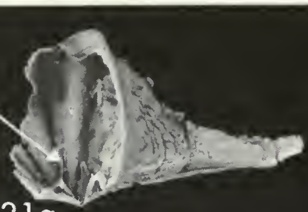
External micro-ornamentation consists of a fine radial lineation (observed only on the silicified specimens), of about fifteen ridges per mm width medially on the ventral valve at about 5 mm from the umbo.

The ventral interarea is high, with a curvature of about 180°, and extends the complete width of the hinge line (Fig. 122a, b); it is irregularly denticulate. The dorsal interarea is short (only about 0·2 mm) and may not extend for the full hinge width.

ONTOGENY. Within the ventral valve of young shells the delthyrium is open but in older valves apical secondary thickening, between the dental plates, partially fills the cavity almost to the level of the interarea (Fig. 122a). This infilling between the dental plates may extend anteriorly in the delthyrium for up to 2 mm. The delthyrium is narrow, its margins diverge at 20–30° and are differentiated from the interarea by shallow grooves and ridges (Fig. 124b), which both represent the traces of the teeth and show that a delthyrial cover was probably present in life. The teeth are triangular in outline and cross section; they do not extend far beyond the hinge line. In early growth stages the teeth were supported by subparallel dental plates about 0·2 mm apart. As the interarea grew anterodorsally, and away from the floor of the valve, the dental plates grew anteriorly only far enough to support the teeth perpendicularly to the valve floor. Thus adult teeth are supported by dental ridges which merge posteroventrally into the dental plates (Fig. 122b). These converge slightly below the interarea and then diverge onto the valve floor within 1 mm on either side of the mid-line. They do not continue anteriorly on the valve floor as ridges, nor is there a median ridge, other than the internal expression of the median sulcus. The muscle scars are indistinct, but the adductor scars were confined posterolaterally, between the dental plates, and extended anteriorly for over half the valve length with a narrowly triangular outline. The diductor scars appear to have flanked the adductor scars and to have remained within the confines of the ventral sulcus. (It may be that the anterior portion of the scars described above as adductors were the anteromedially joined diductor scars. If so the adductor scars extended only a short distance in front of the dental plates and were surrounded anterolaterally by the diductor scars.)

Within the dorsal valve the sockets are shallow, being floored by fulcral plates extending from below the hinge line to the bases of the inner socket ridges (Fig. 125), which diverge at about 75° from each other. A pair of plates diverge dorsally from the inner socket ridges either side of the small longitudinally striate cardinal process. These plates (crural bases) converge slightly towards the valve floor, to which they are fused only posteriorly (Fig. 127b). In larger specimens (about 14 mm wide) the inner socket ridges and crural bases converge to the valve floor more strongly and secondary shell developed apically (Fig. 125). The crura extend subparallel to one another from the anterodorsal extremities of the socket/crural plates, but the form of the spiralia is unknown. A pair of ridges developed during ontogeny which extend anteriorly from the crural bases along the internal edges of the dorsal fold for three-eighths of the valve length (Fig. 125); they enclose the narrowly ovate adductor muscle scars which, in adult valves, were separated medially by a low ridge. With the exception of the ventral umbo and between the dental plates, the shell substance of the valves remained thin; it is impunctate and probably did not include the development of an internal tertiary layer.

DISCUSSION. This species is not common in the Fermanagh faunas, being represented by fifteen incomplete ventral valves, three dorsal valves and two incomplete young shells from the Sillees river locality. This, however, is sufficient to allow a full description of internal morphology for the first time. In addition a specimen of *F. rhomboidea* (B7387) from the Cork area of Ireland was sectioned at narrow intervals and shows internal structures identical with the silicified material. The differentiation and development of new structures during growth is difficult to distinguish owing to the shortage of material. In the ventral valve secondary shell infills the space between the dental plates apically and in two adult valves the bases of the dental plates suddenly widen anteriorly, probably representing the anterolateral growth of the plates around the posterior margins of the adductor muscles. In the older dorsal valves the crural bases fused to



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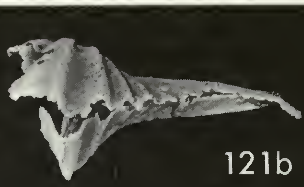

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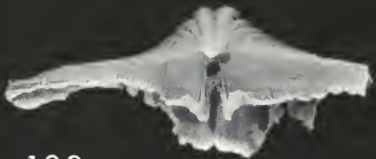

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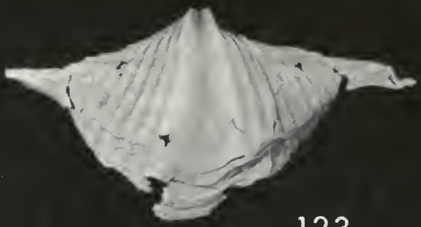

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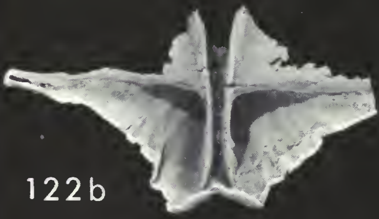

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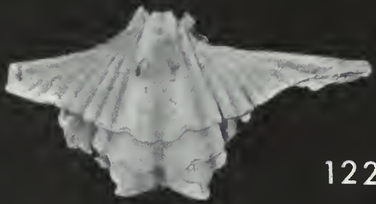

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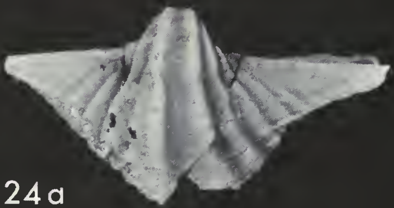

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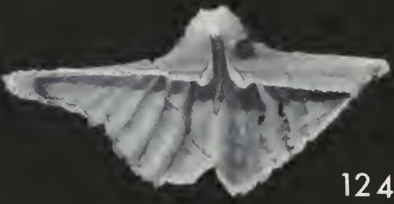
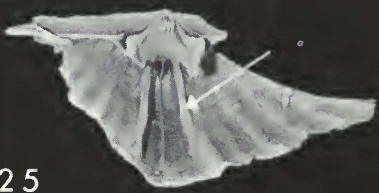


124b



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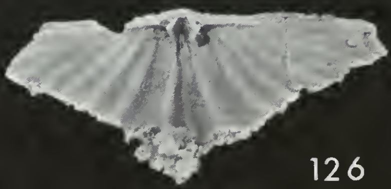

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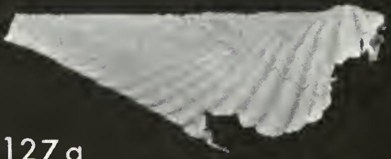

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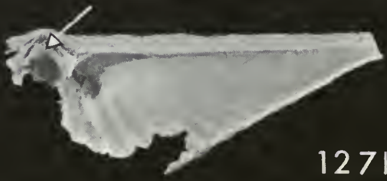


127b

posteriorly prominent ridges bordering the adductor muscle field, and a median ridge, or myophragm, developed between the adductor muscle scars.

Four specimens of *F. rhomboidea* exist in the Gilbertson Collection of the BM(NH), including the lectotype. These are described as coming from Bolland and are probably of low to mid Viséan age. Additional conspecific specimens in the BM(NH) came from low Viséan rocks of north Staffordshire and there is material from the Cork area of Ireland. A single large specimen (B48081) with broken tips to its cardinal extremities (50 mm wide), from the high Viséan of Narrowdale Hill, Staffordshire and labelled *F. grandicostata* (M'Coy), has external characteristics very similar to those of *F. rhomboidea*. Growth lines on this specimen show that at a width of 32 mm the dorsal valve was about 14 mm long and was ornamented by nine pairs of ribs, of which the median pair branched close to the umbo. For a given valve size the ribs are wider on this specimen than on *F. rhomboidea*, and growth lines, developed early in ontogeny, show that a wide fusiform shape did not develop until the shell was at least 15 mm wide. This, the overall size and coarser ribbing distinguishes M'Coy's species *grandicostata* from *rhomboidea*. The internal morphology of M'Coy's species is unknown so it is impossible to be sure of its generic position. However, many of its external characteristics are like those of *Spirifer strangwaysi* de Verneuil, the type species of *Brachythyrina* Frederiks 1929, and if *grandicostata* M'Coy proves to be devoid of dental plates then it should be assigned to that genus.

Other species with which *F. rhomboidea* can be compared are the young of *Spirifer triangularis* J. de C. Sowerby, placed by Muir-Wood (1951) into *Fusella*, but which differ in having a high carinate fold and prominent ventral median rib in the sulcus. Davidson (1858) placed *rhomboidea* into synonymy with *S. convoluta* Phillips, but the latter is distinct in reaching a far greater size and in being more than four times as wide as long. However, growth lines show that when at the size of *F. rhomboidea* the anterior fold of *S. convoluta* was less well developed. The interior of *S. convoluta* is poorly known, but its close dental plates and denticulate hinge line are suggestive of assignment to *Fusella*.

The *Voiseyella* species *anterosa* Campbell, *novamexicana* Miller, *texana* Carter and *mundula* Rowley from Lower Carboniferous strata of Australia and North America all differ in having a more strongly developed imbricate external ornamentation than *F. rhomboidea*. Furthermore, it seems clear that none of the costae branch in these species and their width is commonly about 20 mm (i.e. less than that of mature *F. rhomboidea*). In addition to the above species there are two very similar species, *Spirifer biplicatus* Hall and *S. biplicoides* Weller, from the Kinderhook strata of Iowa, U.S.A. Judged from the external features described by Weller (1914) these species might equally well belong within either *Fusella* or *Voiseyella*. The ventral valve of *S. biplicoides* illustrated by Weller (1914: pl. 39, fig. 29) is very similar to *F. rhomboidea* and dorsal valves have a shallow median groove on the fold, as do the type species of both these genera. There are clear similarities between species of *Fusella* and *Voiseyella* but externally the two groups can be distinguished by the lack of strong, imbricate growth lines on *Fusella* species.

Paucity of material and information on internal morphology of some species inhibits the working out of a phylogeny for *Fusella*. It is possible, however, that a species in the small upper Devonian genus *Strophopleura* gave rise to the Tournaisian species of *Voiseyella* and thence to

Figs 121–127 *Fusella rhomboidea* (Phillips) from Co. Fermanagh. Fig. 121a, b, incomplete juvenile shell viewed dorsally and anteriorly; in Fig. 121a the crura (arrowed) are shown. BB61617, ×6. Fig. 122a–c, incomplete adult ventral valve viewed posteriorly, internally and externally; in Fig. 122a the thickened shell in the apex of the delthyrium has been bored. Note the close, subparallel dental plates. BB61612, ×3. Fig. 123, exterior of a large ventral valve; note the fusiform ears. BB61614, ×2. Fig. 124a, b, exterior and posterodorsal views of a young ventral valve showing asymmetrical growth and, in Fig. 124b, shallow grooving near the delthyrial margin and a bore-hole at the side of the umbo. BB61613, ×5. Fig. 125, internal view of part of an adult dorsal valve showing the cardinalia ridges (arrowed) formed only late in growth. BB61611, ×4. Fig. 126, interior of young dorsal valve with only lightly developed cardinalia. BB61616, ×5. Fig. 127a, b, external and internal views of incomplete dorsal valve showing the diminution of ribs laterally, dorsal interarea and striate cardinal process (arrowed). BB61615, ×3.

the principally Viséan *Fusella*. The Carboniferous to Lower Permian genus *Brachythyrina* may have evolved from this group, as may also the northern species of the Permian genera *Paeckelmanella* and *Pterospirifer*. If so there was an evolutionary trend towards an increase in overall size and, in the Permian, a stronger development of dental plates in these younger genera.

Family **BRACHYTHYRIDIDAE** Frederiks 1919

The family was redefined by Carter (1974) to include only those genera lacking dental plates (adminicula). He included *Brachythyris* M'Coy, *Ella* Frederiks, *Pustuloplica* Waterhouse, *Litothyris* Roberts, *Meristorygma* Carter and *Skelidorygma* Carter. Until Carter defined *Skelidorygma, Brachythyris* had contained species lacking ribs on the dorsal fold (fastigium) and ventral sulcus, as well as those having entirely ribbed shells. Carter placed in *Skelidorygma* those species with entire ribbing, but lacking denticulate hinge lines.

Genus ***BRACHYTHYRIS*** M'Coy 1844

TYPE SPECIES. *Spirifera ovalis* Phillips 1836: 219; pl. 10, fig. 5, from the Viséan of Bolland, Yorkshire. **Lectotype,** here selected, figured by Phillips from the Gilbertson Collection in the BM(NH), B247.

DIAGNOSIS. Hinge markedly narrower than shell width or with wider but very short ventral interarea laterally, commonly denticulate. Simple broad ribs, absent or only weakly developed in sulcus or on fastigium. No dental plates.

DISCUSSION. The type species of *Brachythyris* was not specified by M'Coy (1844) but was designated in 1908 by Buckman who pointed out that the type species, as figured by M'Coy, might be recognized as *Spirifera ovalis*. The illustration to which Buckman referred is figure 20, p. 128 of M'Coy's *Synopsis* (1844) and although this figure is not named, other than by reference to *Brachythyris*, it clearly depicts *B. ovalis*. In George's redescription of the genus in 1927 he quoted *B. ovalis* (Phillips) as type species, and Pitrat, in the *Treatise* (Williams *et al.* 1965), gave the designation as being by M'Coy, and thus accepted the unnamed fig. 20 (1844) as being sufficient indication of the intended type species. Carter (1967) provides a full reference list of the use of the name *Brachythyris*.

Brachythyris ovalis, S. integricostus Phillips and *S. pinguis* J. Sowerby are all somewhat similar species and the morphological differences between them were fully discussed by Davidson (1859). He pointed out that the length to width ratio of these shells is variable, so that although *B. ovalis* is typically longer than wide, in some individuals the reverse is true. This type of variation can be matched in assemblages of Recent brachiopods (McCammon & Bucksbaum 1968). The style of ribbing is characteristic of the genus; well-developed broad, rather flat ribs which do not branch except those that border the ventral sulcus or, less commonly, the dorsal fold, whilst still close to the umbones. In *B. ovalis* the dorsal fold (fastigium) is smooth, whilst weakly-developed costellae may border the sulcus. In *Brachythyris pinguis* the fastigium lacks ribs but has a median groove and the sulcus may be weakly ribbed, especially marginally. The complete ribbing of *S. integricostus* could be considered as one extreme of the variation displayed in this feature by contemporaneous species. Nevertheless, the adult shapes of these three species are distinctive, *B. ovalis* being longer than wide, *S. integricostus* wider than long and *B. pinguis* somewhat quadrate in outline, deep-bodied and more deeply sulcate than the others. The Phillips species *S. duplicicosta* has distinctive finer, branched ribbing, unlike that of *Brachythyris* species. In addition, although its ventral interarea is narrow compared to the width of the shell, it has strong dental plates and so cannot be a *Brachythyris*. Another species having affinities with *Brachythyris* is *S. rotundata* J. Sowerby. Its ribbing is like that of the much smaller *B. ovalis*, but even the juvenile outline of *S. rotundata* seems to have been broader than long, and the adult hinge line is wide, unlike that of *Brachythyris* species as usually defined. A difficulty lies here in the fact that young specimens, up to about 50 mm wide, may have distinctly narrow hinge lines (under 30 mm) and so fall well within the definition of *Brachythris*. As the general characteristics of this species, including its lack of dental plates, indicate to me an assignment to *Brachythyris* I have extended the genus diagnosis to include specimens with wider hinge lines, but only if accompanied by very short ventral interareas, so that the umbones remain close to each other throughout ontogeny. *Spirifer integricostus* Phillips has normally been considered as a *Brachythyris* species, but its entire ribbing fits it better into Carter's *Skelidorygma*. A problem with this assignment is that *S. integricostus* has a weakly denticulate hinge line, while species in Carter's genus should not. As denticulation is not always easy to distinguish I widen the diagnosis of *Skelidorygma* to include *S. integricosta*, a species found rarely in the Fermanagh silicified faunas.

Genus ***SKELIDORYGMA*** Carter 1974

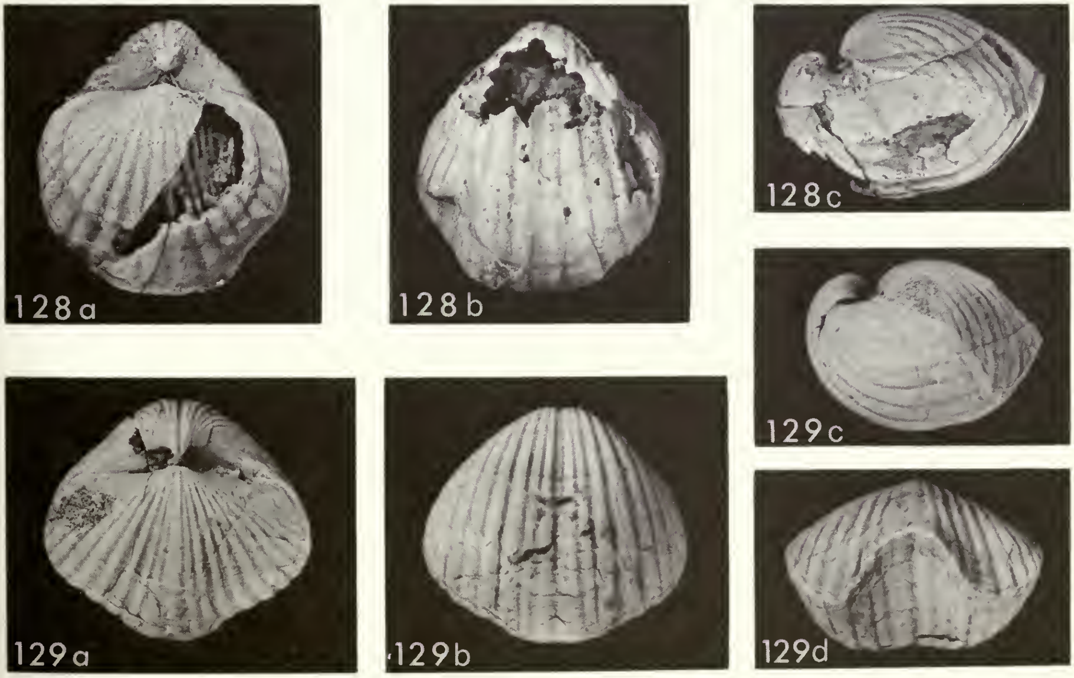
Type species. *Spirifer subcardiiformis* Hall 1858, from the Salem Limestone (Viséan) of mid-continental North America, by original designation of Carter (1974: 692).

Diagnosis. Ovate to subcircular Brachythyrididae, entirely ribbed with simple flattened costae, but branching medially on gentle fold and sulcus. Ventral interarea weakly to not denticulate.

Skelidorygma integricosta (Phillips)
Figs 128, 129

v* 1836 *Spirifera integricosta* Phillips: 219; pl. 10, fig. 2.
1844 *Brachythyris integricosta* (Phillips) M'Coy: 145.
1859 *Spirifera integricosta* Phillips; Davidson: 55; pl. 9, figs 13–19.

Lectotype. Here selected from the Gilbertson Collection, BM(NH), B269, being the specimen figured by Phillips and refigured here (Fig. 129). It is from the Viséan of Bolland, Yorkshire.



Figs 128–129 *Skelidorygma integricosta* (Phillips). Fig. 128a–c, incomplete young shell from Co. Fermanagh; viewed dorsally (showing part of the spiralium), ventrally and laterally. BB63694, ×2. Fig. 129a–d, **lectotype**, here chosen, from the Viséan of Bolland, Yorkshire; viewed dorsally, ventrally, laterally and anteriorly. B269, ×1.

Diagnosis. Broadly to very broadly ovate in outline, strongly biconvex shells. Ventral umbo incurved, close to dorsal umbo, giving concave, weakly denticulate ventral interarea about two-thirds as wide as shell. Ribbing entire, mostly with simple, low, rounded costae widening anteriorly. Micro-ornamentation of non-lamellose growth lines. Small deltidial plates, dental plates lacking. Shell impunctate.

Discussion. Only one almost complete young shell, believed to be of this species, has been collected from the silicified limestone. It is 18·5 mm long, 16·8 mm wide and 12·7 mm thick; it is thus rather more like *Brachythyris ovalis* in outline than the lectotype of *S. integricosta*. However, the entire ribbing and strong biconvexity of the Fermanagh shell are characteristic features of this species rather than of *B. ovalis*.

Although the silicified specimen is broken, so as to allow a view of the brachidium with about nine coils on each side, siliceous deposits in the umbones obscure all details of the cardinalia, making it impossible to add to the descriptions previously given for this species.

The lectotype of *S. integricosta* is about the same size as the holotype of the genotype *Skelidorygma subcardiiformis* (Hall) (Carter 1974: pl. 4, figs 8–12) and both have similar shapes, other than in the dorsoventral outline where the American species is relatively longer. It differs also in having slightly coarser ribs, a non-denticulate hinge line and weaker uniplicate anterior commissure.

Superfamily **SPIRIFERINACEA** Davidson 1884

Family **SPIRIFERINIDAE** Davidson 1884

Genus ***SPIRIFERELLINA*** Frederiks 1919 (1924)

Type species. *Terebratulites cristatus* von Schlotheim, 1816, from the Zechstein of Glücksbrunnen, Thüringen. Lectotype selected by Campbell (1959) from the Schlotheim Collection of the Geologisch-Paläontologisches Institut und Museum, Berlin.

Diagnosis. Very broadly obovate in outline, strongly ventribiconvex in profile. Commonly eight (dorsal valve nine) strong angular plications, with medium sulcus not strongly differentiated. Ventral interarea not extending to maximum shell width. Ornamentation of distinct growth lines and micro-ornamentation of pustules and microspines. Ventral median septum is high posteriorly and extends anteriorly beyond the dental plates, with posteriorly concave anterior edges. Inner socket ridges are supported by plates to the valve floor.

Discussion. Campbell (1959), recognizing the common confusion between *Spiriferellina* and *Punctospirifer* North, redescribed the type species of these genera. He had, however, to rely upon serial sections of specimens for the internal morphology and was unable to be precise about the relationships of the dental plates and median septum in *Spiriferellina cristata*, the type species. The silicified Viséan species *S. insculpta* (Phillips), described below, is very similar to *S. cristata* externally and can be considered to be congeneric.

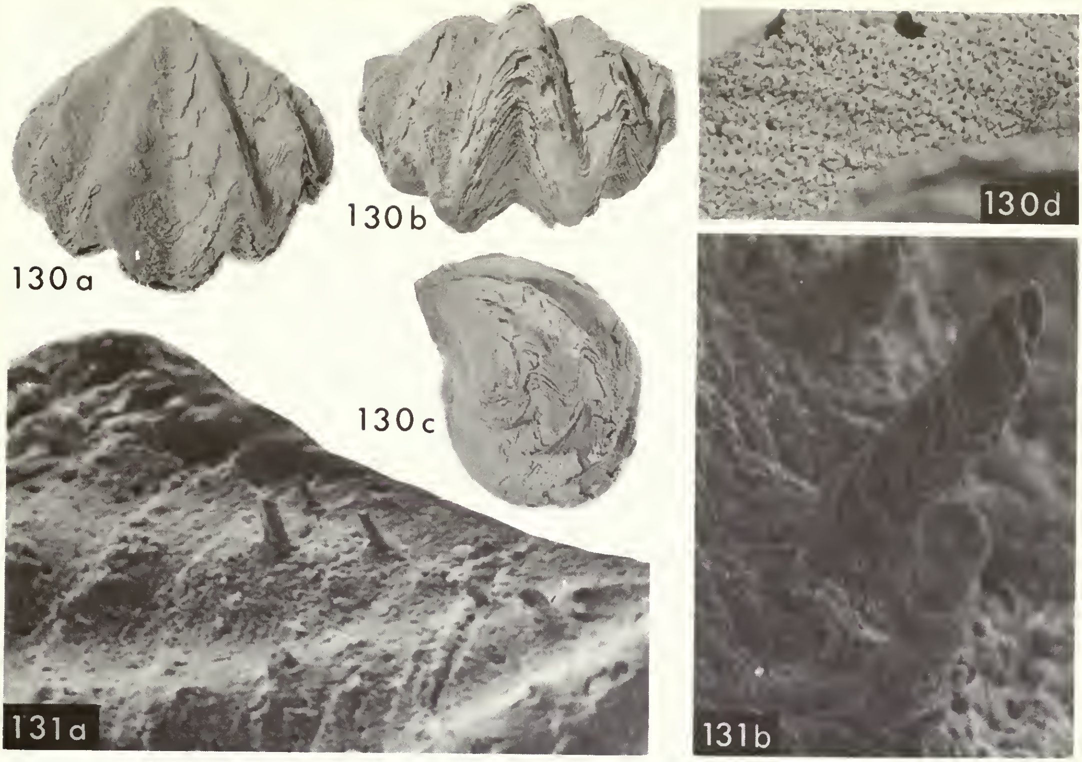
Spiriferellina insculpta (Phillips)

Figs 130–143

v* 1836 *Spirifera insculpta* Phillips: 216; pl. 9, figs 2, 3.
1858 *Spiriferina* (?) *insculpta* (Phillips) Davidson: 42; pl. 7, figs 48–55.
v. 1863 *Spiriferina insculpta* (Phillips); Davidson: pl. 52, fig. 14 (not fig. 15).
1920 *Spiriferina insculpta* (Phillips); North: 217; pl. 13, fig. 11.

Lectotype. Here selected, *S. insculpta* Phillips from the Gilbertson Collection, BM(NH), B304. The specimen comes from the Carboniferous Limestone of Bolland, Yorkshire and was that figured by Phillips in 1836 (Fig. 130).

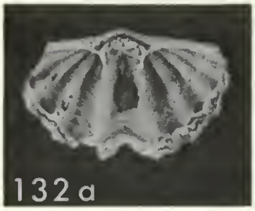
Diagnosis. Transversely broadly elliptical in outline, ventribiconvex in profile with high, only slightly curved ventral interarea. Strong angular costae, normally five or seven on dorsal valve. Weakly lamellose and minutely spinose external ornamentation. Sockets and crural bases elevated above valve floor.



Figs 130–131 *Spiriferellina insculpta* (Phillips). Fig. 130a–d, **lectotype**, here chosen, from the Viséan of Bolland, Yorkshire; viewed ventrally, anteriorly and laterally (with the ventral valve uppermost), ×2, and an enlarged area of the shell showing the endopunctation, ×10. B304. Fig. 131a, b, from Co. Fermanagh, showing details of the microspinous external ornamentation. BB61626, S.E.M. (a) ×50, (b) ×200.

Discussion. For its time Phillips' (1836) original description is quite good – 'Cardinal area large; the mesial and two or three lateral folds very bold, acute, and strongly striated across.' North (1920) gave a full description of the exteriors but was incorrect in suggesting that Davidson (1858) had refigured the type specimen and that the dorsal valve has one more rib (costa) than the ventral valve; in fact the reverse is true. Dorsal valves always have an odd number of costae, one less than ventral valves, a fact that is dictated by the morphology of the commissure (Fig. 130b).

S. insculpta is more rounded in outline than the other *Spiriferellina* species from our Lower Carboniferous rocks and the dorsal valve has a greater convexity than has the closely related species *S. perplicata* (North). Because of this greater curvature the internal morphology also differs. In the flatter valve of *S. perplicata* the sockets and crural bases are close to, and fuse with, the inside surface of the valve; in *S. insculpta* the valve curvature keeps the sockets and crural bases separate from the valve floor (Fig. 132b). On the largest silicified valves traces of muscle scars can be seen on the crural bases (= inner socket plates), which probably represent the sites of attachment of the pedicle adjustor muscles. The dorsal adductor muscle scars are just anterior of the crural bases, within the trough of the dorsal fold and, in adult specimens, are separated medially by a low ridge (Fig. 133). Unfortunately, in no specimen are the spiralia preserved beyond the first dorsomedian primary lamellae; although at a distance of about 2·0 mm from the dorsal umbo there are two ventrally projecting prongs, no jugum has been observed. Campbell (1959) was unable to describe the interior of *S. cristata*, the type species, from the evidence of serial sections; he believed there to be no jugum in *Punctospirifer*, but he recorded one in the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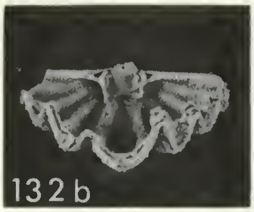
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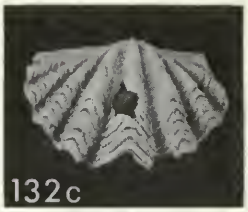
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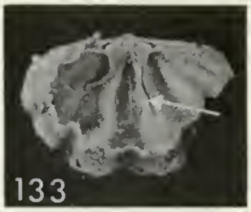
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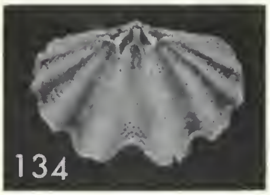
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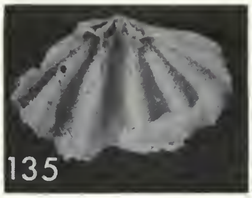
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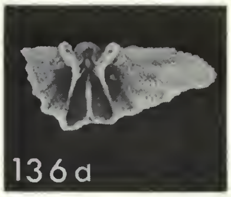
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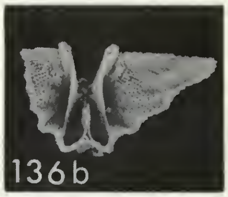
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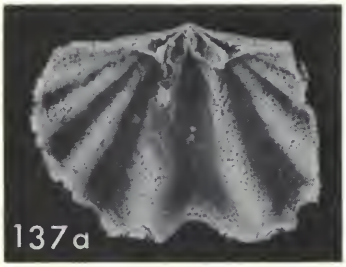
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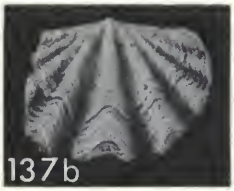
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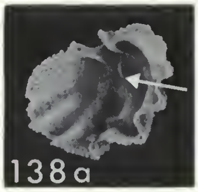
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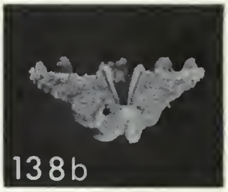
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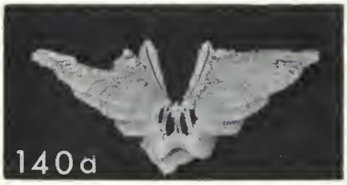
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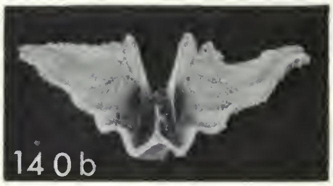
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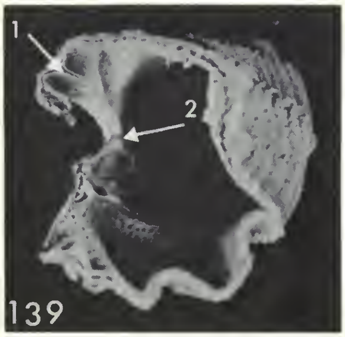

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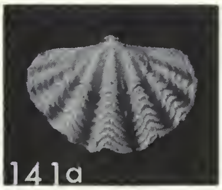
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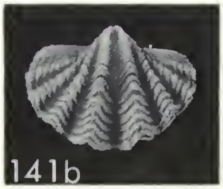
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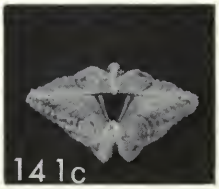
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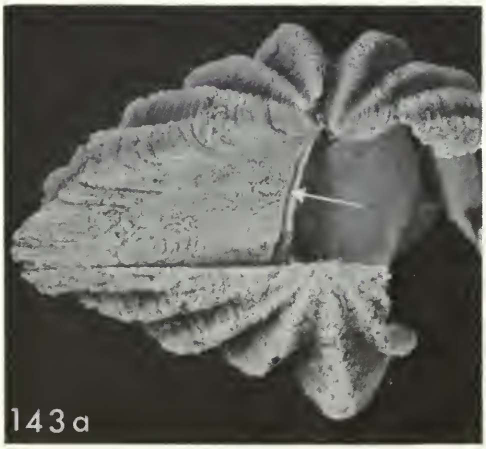
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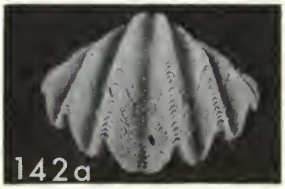
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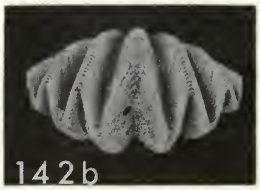
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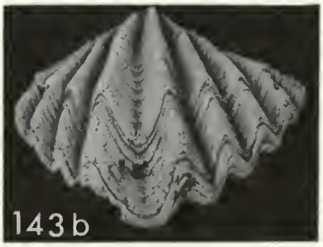
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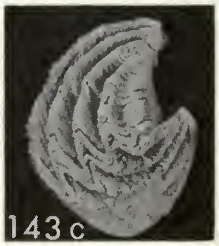
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North American Mississippian genus *Reticulariina*. The evidence afforded by this silicified material is equivocal and it is impossible to say if, in life, a complete jugal saddle connected the two prongs which are preserved in some specimens. At any event the mouth section of the lophophore would have been in this region, close to the body wall.

The ventral valve interior of *S. perplicata*, as seen in silicified specimens described by Brunton & Champion (1974) from Staffordshire, differs only slightly from the Fermanagh specimens of *S. insculpta*. The dental plates are short in both species but those of *S. insculpta* are even less well developed; they recede strongly below the ventral interarea and leave the teeth and distal (dorsal) half of the delthyrial edges unsupported, save for slight dental ridges (Figs 138a, 140b). The anterior edges of the dental plates diverge slightly to the valve floor where they join onto the lateral slopes of the median pair of costae (Fig. 136). In *S. perplicata* the dental plates fuse to the valve floor along the crests of the median pair of costae. The median septum is high posteriorly and sharply truncated anteriorly, approximately at the same position behind the anterior margin of the valve as are the jugal prongs. It seems likely, therefore, that the anterior edge of the ventral median septum also marks the position of the body wall in the living animal. Ventral muscle scars have not been distinguished, but it is probable that the median septum was involved with muscle attachment.

ONTOGENY. The Fermanagh specimens range in width from 1·5 mm to nearly 10·0 mm. In the smallest shells there are only two ventral costae and no dental plates, but the median septum can be distinguished. By a width of 2·0 mm to 2·5 mm minute apical dental plates had started to develop and by a width of 4·0 mm these were clearly differentiated. By this time the full eight ventral costae can normally be distinguished (Fig. 138), and these valves change little during further stages of growth. In a dorsal valve 4 mm wide the cardinal process is difficult or impossible to see, the crural bases remain joined to the valve floor anteriorly and there is no sign of the median ridge. The development of the cardinal process varies considerably, but commonly by a valve width of about 6 mm it can be recognized as an apical, longitudinally striated, low knob. Normally a low median ridge developed anteriorly and the straited myophore region became increasingly posteriorly-directed during the later stages of ontogeny, a period in which the median and posterolateral adductor scar bounding ridges were developed (Figs 132, 135).

The development of the external lamellose ornamentation persisted throughout ontogeny, but posteriorly it was more delicate and abrasion normally made the umbones relatively smooth. Anteriorly the lamellae are prominent, 7 or 8 occurring in each 1 mm on the dorsal median rib. The edges of the lamellae are finely scalloped and rarely microspines are preserved (Fig. 131).

Figs 132–143 *Spiriferellina insculpta* (Phillips) from Co. Fermanagh. Fig. 132a–c, adult dorsal valve viewed internally, posterodorsally and externally. BB63553, ×3. Fig. 133, internal view of shell with most of the ventral valve missing; the cardinalia and one crus (arrowed) can be seen. BB63562, ×5. Fig. 134, immature dorsal valve interior showing the small juvenile crural bases, and endopunctation. BB63556, ×5. Fig. 135, immature dorsal valve interior with the median muscle scars just showing. BB63555, ×4. Fig. 136a, b, incomplete ventral valve viewed internally and posteriorly to show the dispositions of the dental plates and median septum. BB63560, ×4. Fig. 137a, b, young dorsal valve interior, prior to the growth of the cardinal process (cf. Fig. 132a), ×6, and exterior, ×4. BB63554. Fig. 138a, b, juvenile ventral valve viewed ventrolaterally and posteriorly, showing the young median septum (arrowed). BB63561, ×6. Fig. 139, lateral view of an incomplete shell showing the ventral median septum (arrow 1), and a dental plate and its articulation with the inner socket ridge (arrow 2). BB63558, ×8. Fig. 140a, b, incomplete ventral valve viewed posteriorly, with the umbo missing, to show a sectional-like view of the dental plates and median septum, and seen internally. BB63559, ×4. Fig. 141a–c, juvenile shell viewed dorsally, ventrally and posteriorly, showing the lamellose external ornamentation. BB63557, ×4. Fig. 142a, b, complete shell viewed anteroventrally and anteriorly (dorsal valve uppermost); there is a small bore-hole on the ventral valve anteromedially. BB63531, ×2·5. Fig. 143a–c, incomplete adult shell viewed posteriorly, ×4, showing ornamentation of the ventral interarea and groove near the delthyrial margin (arrowed), and ventrally and laterally, ×2. BB63530.

Microspines have only been recorded previously on *Spiriferellina* species by Brunton (1976), although Campbell (1959) described 'nodes' on the exterior of the type species, *S. cristata*, which he said were not the 'bases of spinules'. I agree with Campbell's conclusion but it is now clear that in *S. insculpta*, at least, there was also a microspinous ornamentation during life. The majority of the microspines are not preserved and those that remain are usually between the costae anteriorly or on the posterolateral flanks of ventral valves where the largest seen is 0·5 mm long; only very occasionally have they been seen on dorsal valves and then close to the valve margin. It appears that during early stages of growth, up to a valve width of about 3 mm, the microspines developed principally along the crests of costae (Fig. 131a); scars from where they have broken leave a distinctive pattern. Later in life the microspines developed more regularly along each lamella, with a frequency of about ten per mm, so as to form continuous rows on and between the costae (Fig. 142). Being silicified it is impossible to describe the detailed structure of these spines, but the silica replicas indicate that they were hollow.

Microspines. MacKinnon (1974) has described the spinose ornamentations of the endopunctate Liassic species *Spiriferina walcotti* (Sowerby). He showed that the spines became more densely distributed towards the valve margins, in a similar fashion to those of *S. insculpta*. He also discussed the means of growth of spines of *Spiriferina walcotti* and on *Spinatrypa* specimens. It seems likely that the main distinction between spiriferide and strophomenide tubular spines is that those of the Spiriferida developed by the folding under anteriorly of shell around short-lived marginal epithelial protuberances (Brunton 1976: text-fig. 1), as distinct from the prolonged wholly tubular development in the Strophomenida. When the mantle regressed, prior to the growth of the next lamina, spine growth probably ceased and continued shell deposition covered their internal openings. In particularly well preserved specimens a short indistinct line, immediately anterior of the spine base, marks the position in which the growing mantle margins re-fused.

The purpose of the microspinous ornamentation is not clear; it could have helped anchor the animals into a soft sediment or have been a protective adaptation against small crawling or encrusting predators. As the microspines must have grown at the valve margins, and these regions were probably always clear of the sediment substrate, the former suggestion is less likely than the latter. Most encrusting or boring organisms are likely to have found difficulty in 'sitting' on the external surface of *S. insculpta*; in about 200 valves only ten are bored, seven of which are ventral valves.

Distribution. The species is much more common at the Sillees river locality than at the Carrick Lough locality, although the biggest specimen comes from the latter. In the collections of the BM(NH), specimens of *S. insculpta*, almost identical with the type specimen from Bolland, come from the D Zone 'reefal' limestones of Narrowdale, north Staffordshire. The species is also known from rocks of a similar age in Derbyshire, Anglesey and north-west Ireland. North (1920) indicated that the species, as well as his species *S. perplicata*, was to be found virtually throughout the D Zone. North's (1920) 'mut. K' of *S. perplicata* came from Tournaisian rocks of the south-west province. The extra pair of ribs commonly seen on the Fermanagh specimens of *S. insculpta* (as compared to the lectotype) may indicate a derivation from a pre-existing *S. perplicata*-like stock such as North's 'mut. K'. De Koninck (1887) has recorded the species from high Viséan strata at Visé, Belgium, and Sarycheva & Sokolskaja (1952) list it from near the Viséan/Namurian boundary of the Moscow Basin, but these are somewhat doubtful identifications and otherwise the species appears to be unknown outside the British Isles.

Other *Spiriferellina* species described from Viséan rocks elsewhere are uncommon. From the Utting Calcarenite of north-western Australia (of a similar age to the Fermanagh fauna) Roberts (1971) described *Punctospirifer pauciplicatus*, but the illustrations are quite similar to *S. insculpta* and I think it should be assigned to *Spiriferellina*. Weller (1914) described *Spiriferina salemensis* from the Salem Limestone of Indiana (probably equivalent to early Viséan in age), and this species should probably also be assigned to *Spiriferellina*. Species attributable to the genus do not seem to have been described from Russian faunas of early to mid-Viséan age.

Superfamily **RETICULARIACEA** Waagen 1883

Family **MARTINIIDAE** Waagen 1883

Genus ***MEROSPIRIFER*** Reed 1948 (1949)

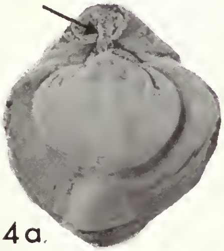
TYPE SPECIES. *Martina (Merospirifer) insolita* Reed 1949: 467, by original designation of Reed (1949: 470).

DIAGNOSIS. Martiniidae with broadly obovate outline and rounded transversely rhombic lateral profile. Indistinct ribs developed late in ontogeny. Dental plates subparallel and close to midline, crural plates lacking.

DISCUSSION. In 1949 Reed described two species under his new subgenus *Merospirifer, M. insolita*, which he stated (1949: 470) to be the type species of his subgenus, and *M. disparilis*; both came from the Charleston Main Limestone of Roscobie, Fife, of high Viséan (P_2) age. The material described by Reed is in the J. Wright Collection of the Royal Scottish Museum, Edinburgh. There are five syntypes of *M. insolita*, but, as Reed (1949: 468) remarked, that numbered 538 is the best specimen and is here selected **lectotype**. This specimen was figured by Reed (1949: pl. 10, figs 6–8) and is refigured here (Figs 146a–c).

Reed gave no separate subgeneric diagnosis but included doubtfully within *Merospirifer* the species *Martinia rhomboidalis* M'Coy, *Martinia galataea* Bell and *M. thetis* Bell. In addition the species *Spirifera linguifera* Phillips should belong to *Merospirifer* and it is to this species that certain poorly-preserved rare specimens from Fermanagh are assigned. *Merospirifer* was recognized as a genus in the Brachiopoda *Treatise* (Williams *et al.* 1965).

Within the Martiniidae the only established genera of Carboniferous age possessing dental plates are *Eomartiniopsis* and *Martiniopsis*, both of which appear to have crural plates, and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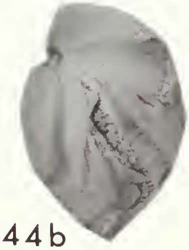
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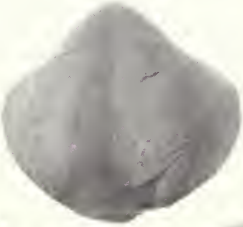
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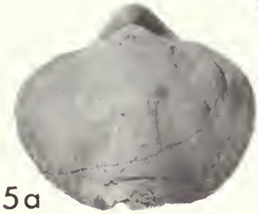
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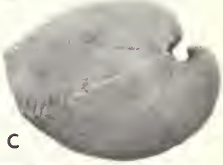
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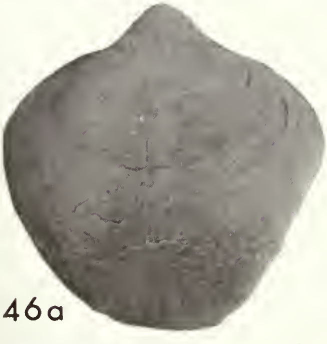
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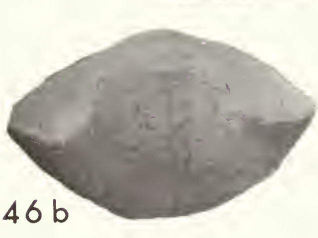
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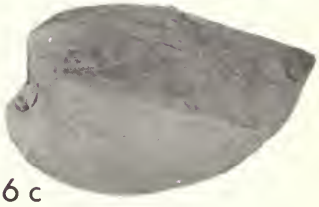
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Figs 144–145 *Merospirifer linguifera* (Phillips). Fig. 144a, b, paralectotype, from the Viséan of Bolland, Yorkshire, viewed dorsally and laterally, showing a dental plate (arrowed) at the broken umbo; the specimen was damaged in life and grew in a distorted fashion. Figured by Phillips (1836: pl. 10, fig. 4). B248, ×1. Fig. 145a–c, **lectotype**, here selected, from the Viséan of Bolland, Yorkshire, viewed dorsally, ventrally and laterally. BB61414, ×1.

Fig. 146 *Merospirifer insolita* Reed. **Lectotype**, here selected, of type species of *Merospirifer*. From the late Viséan of Fife, Scotland, viewed ventrally, anteriorly and laterally. J. Wright Collection, Royal Scottish Museum, Edinburgh, no. 538, ×1.

Martiniella and *Merospirifer* which lack crural plates, but are poorly known through inadequate original descriptions or illustrations. The weak development of ribs and shell outline seem to be characteristic of *Merospirifer*. *Martiniella* Grabau & Tien is described no more fully by Grabau (1931: 420) than by Williams *et al.* (1965) and it is difficult to know whether or not it is synonymous with *Merospirifer* or indeed *Eomartiniopsis* as suggested by Sokolskaya (1941) and Havliček (1959). In the original description of *Crassumbo* Carter (1967), a member of the Reticulariidae, the genus was distinguished from *Eomartiniopsis* by having strongly thickened umbones. Roberts (1971), in describing *Crassumbo* ? *jonesi* from the Lower Carboniferous of the Bonaparte Gulf Basin of north-western Australia, compared it with *Martinia rhomboidalis* M'Coy, but is in error in calling it '*Spirifer rhomboidea* Phillips'. Phillips' (1836) species was not the same as that figured by M'Coy (1844: pl. 22 fig. 11); the former should be assigned to *Fusella* and the latter, as suggested by Reed, might belong to *Merospirifer*.

The geographical and stratigraphical range of *Merospirifer* is difficult to determine owing to the uncertainty of its recognition and relationships with similar genera. In the British Isles it ranges throughout the complete Viséan succession. The name has not been used outside the British Isles and the most closely related species would seem to be of Tournaisian age.

Merospirifer linguifera (Phillips)

Figs 144, 145, 147–149

v* 1836 *Spirifera linguifera* Phillips: 219; pl. 10, fig. 4.
1859 *Spirifera glabra* var. *linguifera* Phillips; Davidson: pl. 12, figs 4, 5.

LECTOTYPE. Here selected, *Spirifera linguifera* Phillips from Bolland, Yorkshire, in the Gilbertson Collection of the BM(NH), BB61414 (Fig. 145).

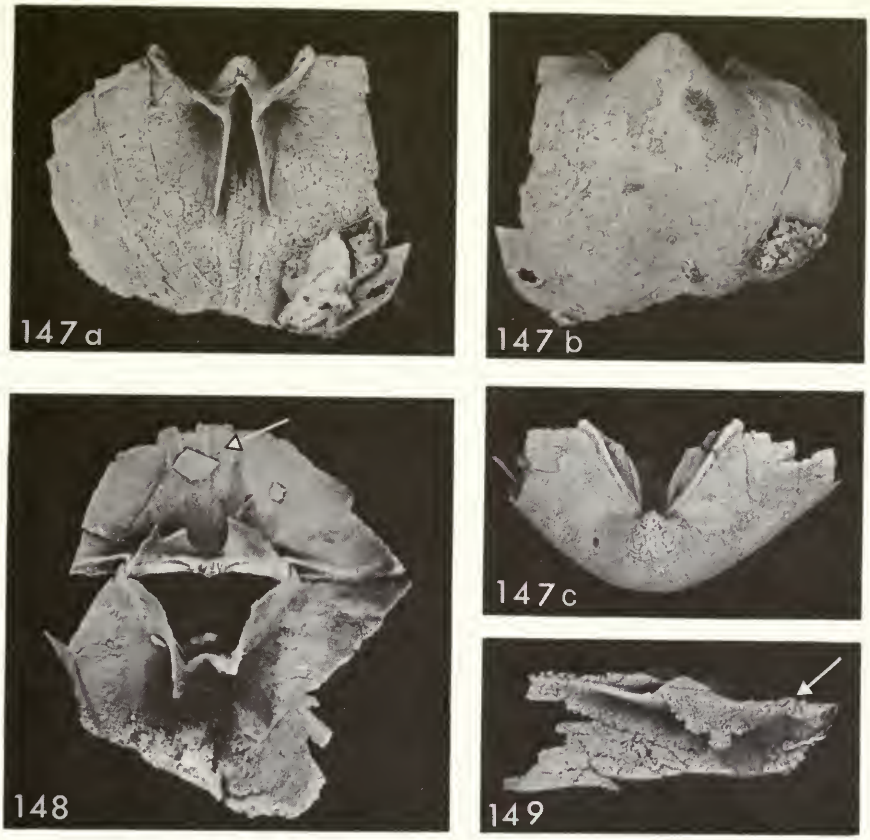
DIAGNOSIS. Relatively wide *Merospirifer* with seven to eight weak ribs on each flank. Ventral adductor muscle scars slightly elevated.

DISCUSSION. The species is represented in the Fermanagh fauna by only six incomplete ventral valves, a pair of articulated umbones (Fig. 148), and fragments. The longitudinally striated cardinal process and virtually smooth exterior places the material within the Martiniidae and the strong dental plates (Fig. 147a) and weak ribbing indicate assignment to *Merospirifer*. Although the Fermanagh specimens are insufficiently complete to determine their outline or profile, the relationship of their umbones, characteristics of the interareas and development of the ventral median sulcus are features closely comparable to those of Phillips' types of *M. linguifera*.

In the Gilbertson Collection of the BM(NH) there are five specimens labelled *linguifera*, two large and three small. One of the large specimens (B248) was figured by Phillips (1836: pl. 10, fig. 4) but is unfortunately somewhat atypical in that the shell is distorted into strongly developed concentric ridges, probably resulting from shell damage (Fig. 144). This specimen also has a broken ventral umbo. The second adult specimen (BB61414) is in good condition and, although not originally figured by Phillips, is the one selected above as lectotype of the species (Fig. 145). Both specimens were figured by Davidson (1859: pl. 12), but he restored the broken specimen and accentuated the ribbing so that the figures are poor representations of the originals.

Phillips' locality is Bolland and the species is quite common in the low Viséan (C_2S_1) mud-bank ('reef') facies of Clitheroe, Lancashire, a few miles east of the true Bolland localities. The same or a very similar species is also to be found in the higher Viséan (D Zone) 'reef' limestones of Staffordshire. These specimens differ from the Scottish material described by Reed in remaining smaller yet being relatively thicker. *M. insolita* also differs in being a relatively larger species than *M. linguifera*.

At the time when Reed described *Merospirifer* the term 'punctation' was used in describing reticulariacean brachiopods; *M. disparilis* Reed was described as perhaps having a punctate shell substance. The term was used in describing the external micro-ornamentation of fine pits found on many of these shells, as well as the shell structural features we now know as endopunctation and pseudopunctation. In 1956 Williams used the term exopuncta in describing



Figs 147–149 *Merospirifer linguifera* (Phillips) from Co. Fermanagh. Fig. 147a–c, incomplete ventral valve, interior, exterior and posterior view; note the convergent dental plates below the delthyrial margins before they bend ventrally and diverge slightly to the valve floor. BB63691, ×2. Fig. 148, conjoined umbones viewed internally showing the cardinalia (but with broken crura), articulation and broken dental plates; the dorsal adductor muscle scars can be seen (arrowed). BB63692, ×5. Fig. 149, fragment of dorsal valve showing the socket, inner socket ridge and cardinal process (arrowed). BB63693, ×5.

superficial pits penetrating no more than the primary shell layer, i.e. a form of external micro-ornamentation. Although some *Merospirifer* species may be slightly exopunctate, none is endopunctate.

Family **ELYTHIDAE** Frederiks 1919 (1924)

Genus ***PHRICODOTHYRIS*** George 1932

Type species. *P. lucerna* George 1932: 546; pl. 35, figs 2a–d; by original designation. Holotype in the Burrows Collection, Sedgwick Museum (No. 371), from the Viséan (D_2) of Lowick, Northumberland.

Discussion. George fully described the genus in 1932 and besides the type species described five new species, *P. ericus, P. insolita, P. paricosta, P. periculosa* and *P. verecunda*. He redescribed the species *Terebratula* ? *lineata* J. Sowerby (1822: pl. 335, figs 1, 2; see Muir-Wood 1951: 105) and assigned it also to his genus, but it has since been made the type species of *Martinothyris* Minato 1953 on account of its dental and crural plates. In 1971 Thomas, following Maxwell's lead (1961), called into question the validity of *Martinothyris* because Muir-Wood (1951) had suggested that *P. lineata* (J. Sowerby), with lectotype no. B60997 in the Sowerby Collection, BM(NH), lacked dental plates. This then contradicted the characteristic feature, the presence of dental plates, by which Minato separated his genus from *Phricodothyris*. On this basis Thomas (1971) correctly concluded that George's (1932) specimen assigned to *lineata* did not belong to that species and consequently that *Martinothyris* was invalid.

While discussing the specimens illustrated by Sowerby, Muir-Wood (1951: 105) wrote that there was an 'apparent absence of apical plates.' However, careful inspection of the lectotype shows reasonably conclusively that there are dental plates, and possibly also short crural plates, as illustrated by George (1932: fig. 6) in a specimen from Treak Cliff, Derbyshire. Thus, although the Sowerby specimen of *lineata* invalidates George's neotype it supports the description he gave of this species which was used by Minato in describing *Martinothyris*. There is, therefore, both a valid type species for this genus and a valid lectotype of that species.

The type specimens of all George's five species came from D Zone rocks of northern England or Scotland and were characterized by outline, whether transverse, equidimensional or elongate; the form of the anterior commissure; the degree of biconvexity; and the spacing of the spine-bearing lamellae. Unfortunately, there is insufficient well-localized material to test the validity of these species, but observations support George's work. The genus is represented in low Viséan rocks and extends into the Permian where the characteristic barbed spines have been beautifully illustrated on Bolivian specimens (Samtleben 1971).

Minato (1953; see also Minato & Kato 1963) erected the genus *Nebenothyris*, based upon *Spirifer (Reticularia) lineata* Nebe (*non* Martin), characterized by possessing 'a prominent median septum in the ventral valve . . . and a septum in the dorsal valve.' Otherwise *Nebenothyris* was said to resemble *Phricodothyris*. The true nature of specimens within this group having at least a low ventral median ridge is being investigated in an attempt to check the validity of *Nebenothyris*. Until that study is complete, and despite the low ventral ridge in the Fermanagh specimens, I retain their position in *Phricodothyris*.

Phricodothyris verecunda George
Figs 150–159

HOLOTYPE. A specimen from the D_2 zone (Brachiopod Beds) of Chrome Hill, Derbyshire, in the P. Roscoe collection of the BM(NH), B46709. Figured by George (1932: pl. 35, figs 3a–d).

DIAGNOSIS (George 1932). An equidimensional biconvex rectimarginate form, in which the spine-bearing growth-halts are regularly distributed over the surface.

DESCRIPTION. George's original description seems to have been based only upon the holotype. The Fermanagh silicified material came principally from the Sillees river locality and comprises six shells plus numerous incomplete dorsal and ventral valves. This material is assigned to *P. verecunda* on account of its equidimensional outline, strongly biconvex lateral profile with a

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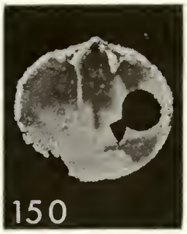
Figs 150–159 *Phricodothyris verecunda* George, from Co. Fermanagh. Fig. 150, juvenile dorsal valve interior showing the young inner socket ridges and one crus; the valve is bored. BB63441, ×7. Fig. 151, incomplete young shell viewed anterolatrally, showing parts of the spiralia. BB63442, ×4. Fig. 152a, b, incomplete young, highly bored, ventral valve exterior and interior to show the 'blisters' of shell repair on the inner surface. BB63443, ×4. Fig. 153, part of dorsal valve exterior showing the typical spinose ornamentation of the genus; the upper and lower arrows indicate the different appearances of the 'spine' bases according to the degree of abrasion. BB63444, ×4. Fig. 154a–c, incomplete dorsal valve viewed externally, showing ornamentation, and internally, ×4, and detail of the cardinalia, ×6. Note also the characteristic internal ornamentation. BB63440. Fig. 155a, b, incomplete ventral valve interior, showing dental ridges and median ridge, ×4, and posteriorly, showing the small interarea and ridges at the delthyrial margins, ×6. BB63438. Fig. 156, conjoined umbones showing the valve articulation. BB63439, ×4. Fig. 157, lateral view of complete shell. BB63436, ×1·5. Fig. 158a, b, an almost complete shell viewed ventrally, ×2·5, and obliquely illustrating the delthyrial region, ×5, showing the external ornamentation. BB63437. Fig. 159, almost complete shell viewed posterodorsally. BB63436, ×3·5.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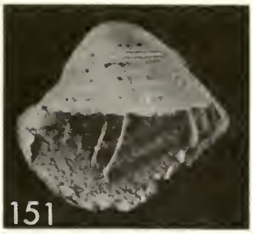
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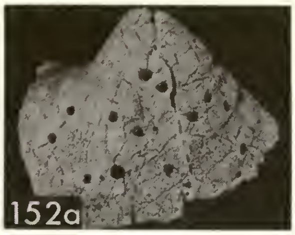
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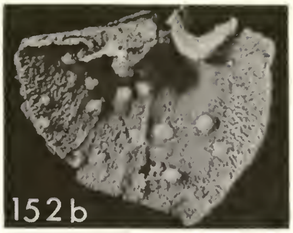
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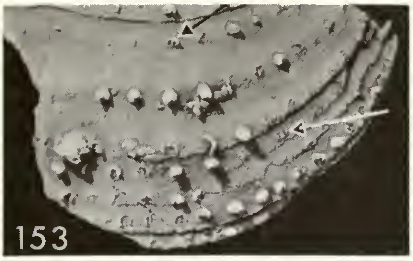
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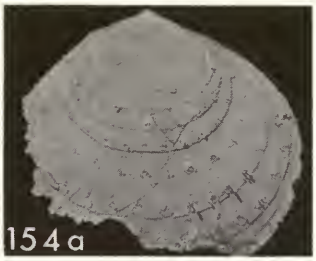
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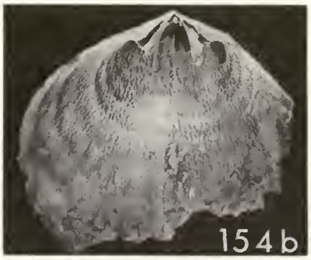
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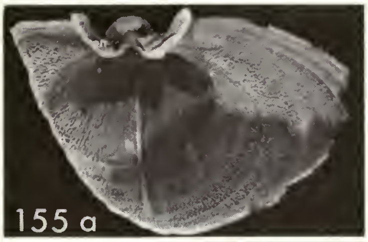
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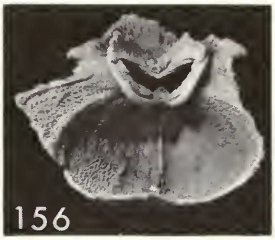
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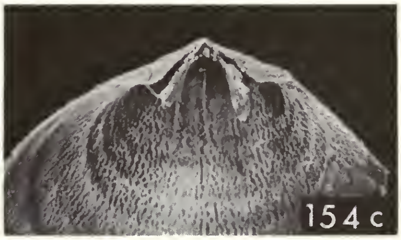
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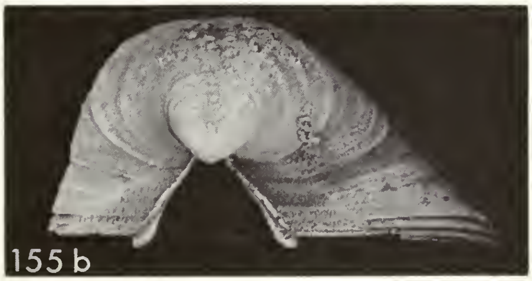
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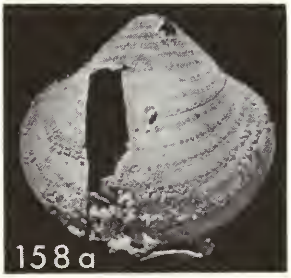
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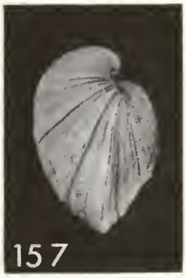
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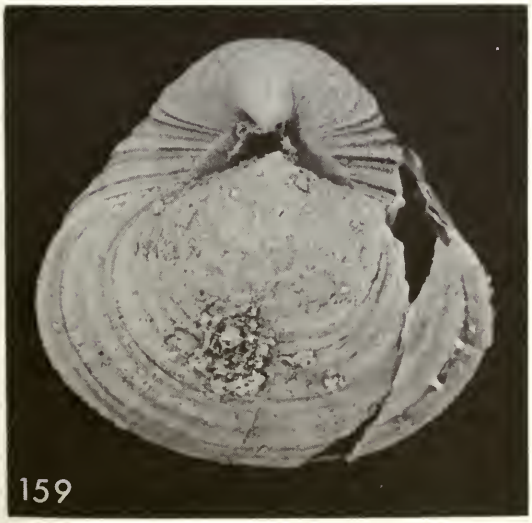
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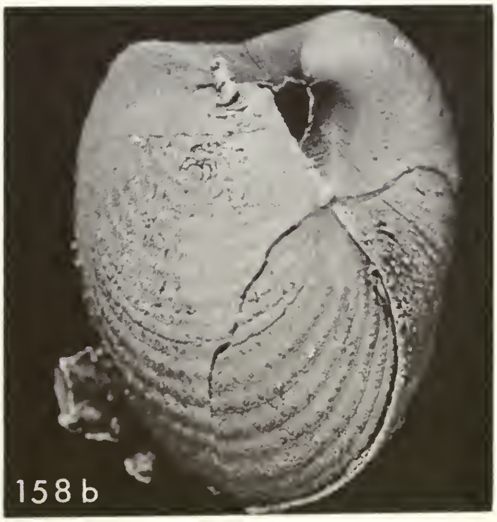

158 b

prominent ventral umbo, and rectimarginate anterior commissure. The external ornamentation differs from that of the holotype, in which George records 14–16 growth lamellae in a length of 10 mm. The frequency of spine-bearing growth lamellae in the Fermanagh specimens varies considerably according to position on the shell and the size of the shell. Posteriorly and again on some individuals marginally, these lamellae are more crowded than over the anteromedian sectors of the valves, where 7–11 lamellae occur in a length of 10 mm. Similarly the lateral frequency of spine-bases on any one lamina varies (compare Fig. 153 with Fig. 158b). The holotype has an eroded surface but has 35 to 40 spine bases in a width of 10 mm. On the Fermanagh shells the frequency varies from 11 to 25 in 10 mm width.

The interiors of valves more than about 10 mm wide are marked, especially posteriorly, by a characteristic pitting (Figs 154b, 155a), which in areas of muscle attachment is modified to a series of sinuous elongate grooves. The ventral valve is aseptate, the teeth being supported only by dental ridges and a low median ridge never developed to more than a fraction of a mm in height (Fig. 155a). Within the dorsal valve the sockets are floored by horizontal fulcral plates extending from the valve walls to the dorsally slightly convergent crura (Fig. 154b, c). These are unsupported and poorly differentiated from the inner socket ridges. The diductor muscle attachment area is apical, small and typically spiriferide in being longitudinally striate or tuberculate (Fig. 156). The dorsal adductor muscle scars are separated by a low ridge which is persistent throughout ontogeny, and in older valves the lateral margins of the scars are confined by a pair of similar low ridges.

Discussion. Valves down to a width of about 2·5 mm can be recognized easily. At this size dorsal valves have an indistinct median ridge extending almost to the anterior margin; the diductor muscle attachment area is indistinguishable (Fig. 150). The inner socket ridges diverge at about 90° from each other in juvenile valves and only increase their angle of divergence to about 100° in the oldest observed valves. The ridges lateral to the adductor scars are visible in valves 9·0 mm wide and from then on became more prominent.

Ventral valves are devoid of any strongly developed morphological features and it is difficult to recognize any ontogenetic changes other than the above-mentioned pitting of the internal surface and greater prominence of the median ridge in old shells. The muscle scars are ill-defined even in the large valves, but it seems that the adductor scars are narrowly ovate and flanked by rounded triangular diductor scars extending anteriorly for just over half the valve length. At their widest point, anteriorly, the diductor scars are about one-third of the total valve width.

The evidence from the silicified specimens indicates that the delthyrium remained open throughout life (Fig. 158b, 159), in which case the pedicle may have remained functional as the principal means of attachment to the substrate. If so, the lack of abrasion at the umbones indicates that the substrate was probably soft and, as George (1932) pointed out, the spine morphology would appear to be suited to function as anchors within the sediment. However, the examination of conjoined umbones shows that the greater part of the delthyrial opening would have been blocked by the dorsal umbo when the shell was open (Fig. 156). The maximum angle through which the shell could have opened is dictated by the disposition of the dorsal and ventral interareas and this varies from 25° to 40°. If in life the gape was of about 30° this would have brought the dorsal umbo into the delthyrial opening, leaving only a few tenths of 1 mm apically through which a pedicle might have emerged. Thus although the species was probably attached by the pedicle when young it seems likely that older shells, provided with barbed spines, relied upon these to 'hold' into the sediment. This corona of spines, extending well beyond the margins of the shell, could also have inhibited predation. If so it appears to have been reasonably successful in that only two specimens in about 50 have been bored. This compares with 30% to 50% of the valves of some relatively smooth productacean and chonetacean species from the same fauna (Brunton 1966a). The two specimens of *P. verecunda* which are bored are illustrated; the hole in the juvenile dorsal valve (Fig. 150) resembles those thought to have been produced by carnivorous gastropods. The holes in the old ventral umbo (Fig. 152) resemble those produced in some living shells by the boring sponge *Cliona*. Dr D. George (BM(NH), Dept. of Zoology) suggests to me that the burrowing polychaete *Polydora* would be expected to produce less circular, more elongate or dumbbell-shaped burrows in the shell. These borings were for habitation and the living brachiopod reacted to the boring by depositing pustules of shell internally (Fig. 152b). Externally the holes are about 0·3 mm in diameter, circular and may have somewhat bevelled edges. In some instances it appears that the cavity within the pustule of shell is slightly larger than the opening at the original shell surface. The minute branching infestation of burrows on the outer surface (Fig. 152a) are those I previously (1966a) thought to have been made by ctenostome bryozoans. More recently work by Voigt (1975) indicates that the ichnogenus *Talpina*, resembling these burrows, resulted from the activities of phoronids.

Family **VERNEUILIIDAE** nov.

Diagnosis. Transverse to subcircular spiriferaceans with equibiconvex profiles. Opposite folding forming ligate to metacarinate anterior margins. Ventral interarea narrow to full width of shell, with open delthyrium or apically restricted by a deltidium. A pair of prominent costae bordering the median sulci, with or without a pair of weaker lateral costae. Micro-ornament apparently of growth lines only. Spiralia laterally directed. Shell substance impunctate.

Discussion. The family includes the genera *Verneuilia* Hall & Clarke, 1894 and *Minythyra* nov., and ranges from mid-Devonian through the Lower Carboniferous.

Verneuilia was not placed in a family in the *Treatise* (Williams *et al.* 1965) and remains a poorly known genus. The type species, *Spirifer cheiropteryx* d'Archaic & de Verneuil 1842, came from the mid-Devonian of Germany, but the name originally also included specimens from the Carboniferous of Visé, Belgium. These specimens were separated as *S. oceani* by d'Orbigny (1850), leaving the much wider Devonian form for the type species. *Verneuilia oceani* is a rare species, seldom if ever figured since de Koninck (1887). One of the three specimens in the Davidson Collection of the BM(NH), B7923, from the type area of Visé, Belgium, is here selected as **neotype** (Fig. 160).

The impunctate shell and spiralia place the family in the Spiriferacea. The development of a persistent ventral interarea precludes the possibility of these genera being assigned to the Athyrididae, although from their outline shapes they resemble some athyrids. The unusual shapes and opposite folding also resembles some Mesozoic zeilleriid terebratulids, such as *Cheirothyris* or some *Zeilleria* species, and it seems that the shape is one that has been repeated occasionally during the evolution of brachiopods in otherwise unrelated stocks.

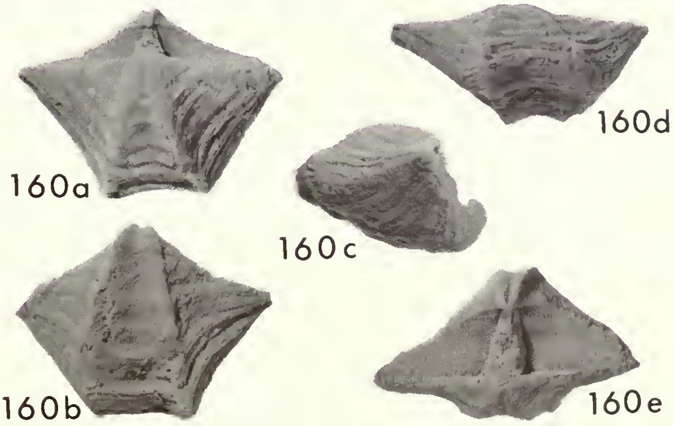


Fig. 160 *Verneuilia oceani* (d'Orbigny). Dorsal, ventral, lateral, anterior and posterior views of the **neotype**, here selected, from the Viséan of Visé, Belgium; Davidson Collection. The specimen closely resembles the illustrations of the species de Koninck (1887) and this is probably the first time the species has been photographically illustrated. B7923, ×3.

Verneuilia has a wide, high ventral interarea which, at least in *V. oceani*, has the vertically disposed microcrenulations in the shell material commonly described as a fine denticulation, and typical of many spiriferaceans. The delthyrium is closed apically by a short deltidium, but the genus remains unknown internally.

Genus ***MINYTHYRA*** nov.

Type species. *Minythyra lopha* sp. nov.

Diagnosis. Minute, subcircular, equibiconvex spiriferids. Both valves with prominent median sulci, bordered by strong ridges (costae), less distinct costae on flanks. Open delthyrium in apsacline interarea. Hinge line up to one half full shell width. Micro-ornament lacking. Laterally directed spiralia, no median septum. Shell impunctate.

Name. Greek, *μινύς* = little or small, + *θύϱα* = door. Fem.

Discussion. The minute shells, from the silicified fauna, assigned to this genus cannot be considered as the young of any other species in the fauna. Externally *M. lopha* sp. nov. might be thought similar to the young of *Hustedia ulothrix*, but that species is distinct in being endopunctate and in having an apical pedicle foramen.

The impunctate shell and spiralia place the genus in the Spiriferida. The external outline is reminiscent of the young of some Devonian athyrid genera, such as *Anathyris* and *Pradoia*, or of the Carboniferous genus *Verneuilia*, with which I place *Minythyra* in the Verneuiliidae. *Verneuilia* is characterized by similar median sulci and bordering costae to *Minthyra*, but differs in having a very broad hinge line, forming much the widest part of the shell, a wide and high ventral interarea, and no flanking costae.

In addition to the type species I assign *M. ernea* sp. nov. and *Rhynchonella opposita* White & Whitfield 1862 (Figured by Weller, 1914: pl. 82, figs 11–13, as *Composita opposita*) from late Kinderhook beds of Iowa, U.S.A., to *Minythyra*.

Minythyra lopha sp. nov.

Figs 161–168

Diagnosis. *Minythyra* with a metacarinate outline resulting from strong costae bordering median sulci, plus a weaker pair of flanking costae.

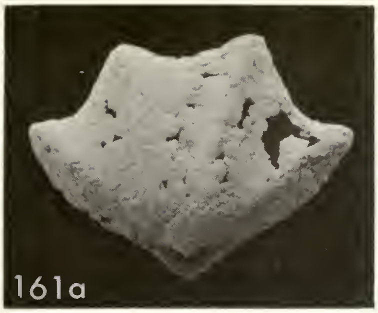
Name. Greek, *λόφος* = crest or ridge, referring to the strong costae.

Locality. Sillees River.

Holotype. BM(NH) specimen no. BD147, figured here as Figs 161a, b.

Material. The holotype plus 40 other complete and incomplete silicified specimens, BB65054–BB65063 and BD135–BD149. Length range from 0·8 mm to 1·2 mm.

Description. Minute, transverse and strongly emarginate shells reaching 2 mm wide and 1·2 mm long. The valves have opposed folding, forming a metacarinate outline and anterior margin (Williams *et al.* 1965: H63) (Figs 162, 163). The costae bordering the median sulci are stronger than the flanking pair. The profile is equibiconvex with an apsacline ventral umbo extending beyond the low anacline dorsal umbo (Fig. 167). An open delthyrium is set in the interarea which extends to approximately one-third of the maximum shell width. The exteriors lack surface ornamentation or growth lines. Internally the only distinguishable features are the teeth, sockets and traces of spiralia (Fig. 166). The teeth are short, but relatively broad knobs protrude from the dorsal corners of the delthyrium. These fit against stout thickenings of the dorsal hinge line, on each side of the umbo, which extend anteroventrally as low inner socket ridges (Fig. 168). (For discussion see below.)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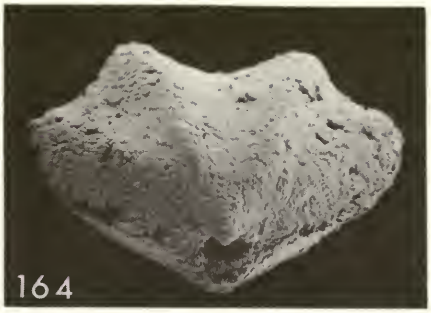
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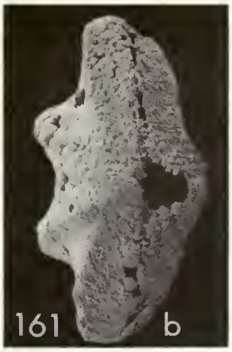
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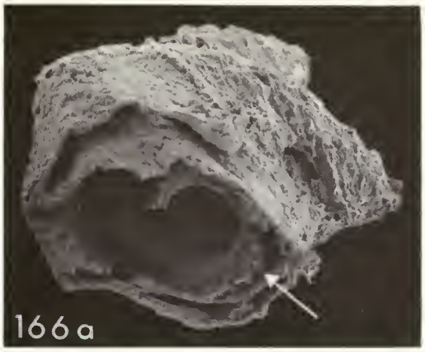
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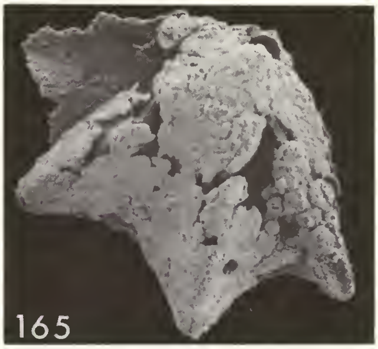
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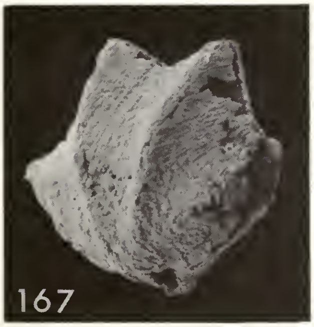
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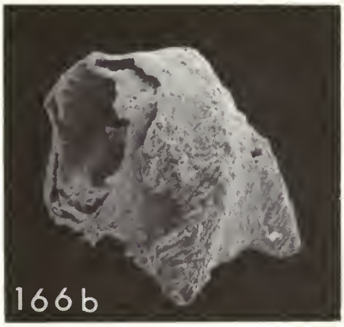
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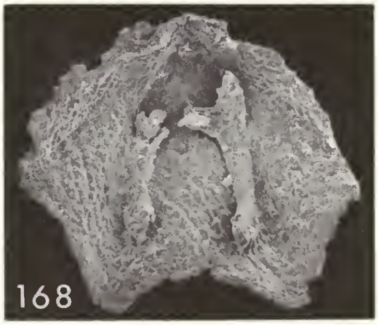
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Figs 161–168 *Minythyra lopha* gen. et sp. nov., from Co. Fermanagh. Fig. 161a, b, **holotype**, posterodorsal and posterior views. BD147, S.E.M. ×20. Fig. 162, dorsal view of complete specimen. BD137, ×7. Fig. 163, posterior view of complete specimen. BD135, ×7. Fig. 164, posterodorsal view of complete specimen. BD144, S.E.M. ×28. Fig. 165, dorsal view of incomplete shell. BD141, S.E.M. ×27. Fig. 166a, b, incomplete shell seen laterally, S.E.M. ×29, and anterolaterally, S.E.M. ×22; the ventral valve is uppermost and part of a spiralium can be seen on which spinose outgrowths (arrowed) developed on the anterior part of the whorls. BD145. Fig. 167, shell viewed dorsolaterally. BD142, S.E.M. ×21. Fig. 168, dorsal valve interior showing shallow sockets (arrowed) and initial sections of the spiralia, including the incomplete jugum; the silica of the internal surface appears to have replicated a mosaic of secondary shell fibres. BD146, S.E.M. ×26.

Minythyra ernea sp. nov.
Figs 169, 170

DIAGNOSIS. *Minythyra* with subcircular outline and narrow ventral interarea. The costation is weak.

NAME. From Lough Erne, Co. Fermanagh, in the region from which the specimens were collected.

Locality. Sillees River.

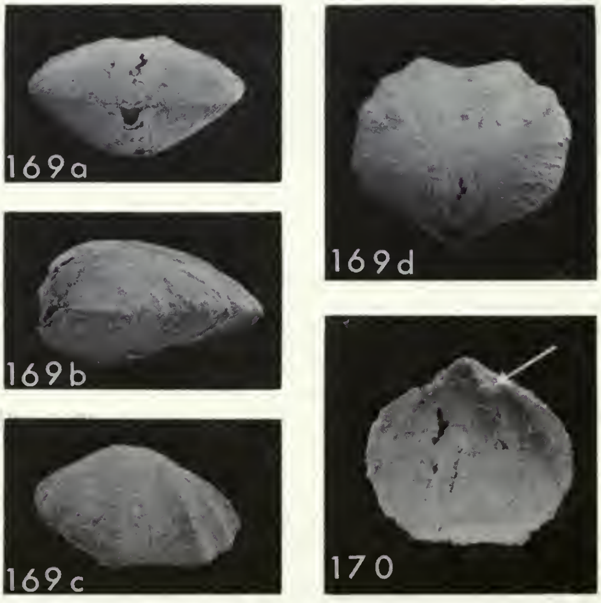
Holotype. BM(NH) specimen no. BD133, figured here as Fig. 169a–d.

Material. The holotype plus 20 other specimens, BD99–BD108 and BD125–BD134. Length range from 1·1 mm to 1·8 mm.

Description. Outline subcircular to transversely broadly elliptical with a weakly bilobate anterior commissure. Profile is equibiconvex, with a narrow apsacline ventral interarea, mostly occupied by the delthyrium. The median sulci and bordering costae are weakly developed. On the flanks a second pair of faint costae are positioned anterior to the place of maximum width. Articulation is by knob-like teeth (Fig. 170) and sockets.

Discussion. The two species of *Minythyra* in the silicified faunas are similarly sized, but readily distinguished by the strongly trisinuate outline and strongly developed costae in *M. lopha*, as compared to the more rounded outline and weak costation in *M. ernea*. The Kinderhookian (Tournaisian), North American species *M. opposita* (White & Whitfield) is unknown internally, but belongs here more happily than in *Composita*, to which it was assigned by Weller (1914). It is a trisinuate shell anteriorly, with costation similar to *M. lopha*, but posteriorly the umbonal angle is not more than 100°, while that of *M. lopha* is in the range of 110° to 120°. It would seem that the North American species has a narrow hinge line, since an interarea is not described, despite the shell dimensions reaching 5·5 mm long and 6·0 mm wide (Weller 1914).

One must always have doubts whether small specimens such as these are valid as true species, and not to be interpreted as the young of other species. However, until a species is found to which these shells can be assigned it is more practical to consider them as independent taxa. While the possibility exists that the young from a recently arrived spat fall, of a hitherto unknown species, might have been entombed in the area, the known presence of minute species of brachiopods in the fossil record and in modern seas makes the likelihood of these specimens representing distinct species all the greater. In Recent British waters species of *Argyrotheca* and *Gwynia* reach only a few mm in length when fully grown.



Figs 169–170 *Minythyra ernea* gen. et sp. nov., from Co. Fermanagh. Fig. 169a–d, **holotype**, posterior, lateral, anterodorsal and dorsal views; the small ventral interarea can be seen, but the medial lineations may be a replication of shell fabric rather than original ornamentation. BD133, S.E.M. ×20. Fig. 170, inside of ventral valve showing a tooth (arrowed). BD134, S.E.M. ×20.

The absence of distinguishable growth lines on these Fermanagh species, despite their preservation on other species, indicates that *M. lopha* and *M. ernea* are young, in the sense that they have not experienced the shell growth halts seen on most larger shells. However, in the fauna as a whole some species, such as the externally rather smooth *Crurithyris urei*, show few growth lines until several mm in length while, by contrast, specimens of the lamellose *Cleiothyridina fimbriata* show many growth lines from a length of about 0·5 mm. Thus both speed of shell growth and external ornamentation have to be considered in the question of the state of maturity or age of *Minythyra* specimens. Since species of *Crurithyris* and *Nucleospira* display occasional growth lines at shell lengths of less than 1 mm, whereas *Minythyra* species do not, it seems that the latter may have grown rapidly to their preserved size within a single growth season. The consistent small size and small total number of specimens recovered from the acid-developed blocks is suggestive of a single assemblage in the area, as distinct from an established population persisting through the time of deposition of the limestone bed from which they came.

Order **TEREBRATULIDA** Waagen 1883

Despite the classical works of Cloud (1942) on Silurian and Devonian terebratulids, Campbell (1965) on Permian taxa, and of Stehli (1956, 1961, 1965), our knowledge of west European Lower Carboniferous species remains slight. Certain generic and specific names, such as *Dielasma hastata*, abound in the literature so widely that they now represent 'sack' taxa representing genera besides *Dielasma* (see Brunton 1982), and are in need of revision. The problem in the classification of these species is that the external shapes of several are very similar and only by studying internal structures can their true identity be recognized. Thus, from the typical limestones of the European Lower Carboniferous it is necessary to section specimens serially, or use acid-developed material, in order to demonstrate the nature of the cardinalia, the loop and presence of dental plates. Only then can correct generic assignments be made.

There is a generalization which may help to distinguish specimens of the short-looped Terebratulidina from the long-looped Terebratellidina which seems to hold good at least in the Carboniferous. When the loop cannot be seen, or is broken, it is noteworthy that taxa of the long-looped Cryptonellidae, the only Palaeozoic members of the suborder, have less incurved, straighter to suberect ventral umbones than do short-looped taxa. In addition the pedicle foramen tends to be more within the delthyrium than in short-looped forms and, at least in European Carboniferous species, the density of endopuncta is much greater in *Cryptonella* than in short-looped species.

Using the *Treatise* (Williams *et al.* 1965) classification it is possible to recognize four distinctive genera and species, three short-looped Dielasmataceans (*Girtyella, Alwynia* and *Beecheria*) and one long-looped Cryptonellacean (*Cryptonella*). Work by Dagys (1972) led him to reclassify terebratulids so that loop length was less important than the ontogeny and form of the cardinalia as a whole. From his studies Dagys suggested seven superfamilies in the Terebratulida, the Stringocephalacea, Cryptonellacea, Dielasmatacea, Terebratulacea, Dallinacea, Loboidothyracea and Terebratellacea. Of these, Cryptonellacea and Dielasmatacea are present in the Carboniferous, where they include the following European genera:

Cryptonellacea:

- Cryptonellidae
  - *Cryptonella**
- Cranaenidae
  - *Girtyella**
  - *Harttella*
- Notothyrididae
  - *Alwynia**

Dielasmatacea:

- Dielasmatidae
  - '*Dielasma*'
  - *Balanoconcha*
- Heterelasminidae
  - *Beecheria**

*Present in this Fermanagh fauna.

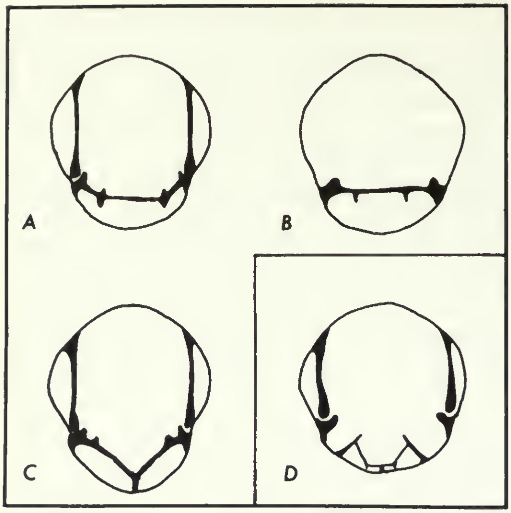


Fig. 171 Stylized cross sections of *Cryptonella* (A), *Alwynia* (B), *Girtyella* (C) and *Beecheria* (D); A–C are cryptonellaceans while D is a dielasmatacean. Ventral valves are drawn uppermost. The sections illustrate the differences in the disposition of the crural bases to the outer and inner hinge plates – they project dorsally and ventrally in *Cryptonella*, dorsally in *Alwynia* and ventrally in *Girtyella*. In *Beecheria* the crural bases are supported by thickened outer hinge plates, the inner hinge plates forming an almost sessile septalium containing muscle scars.

In this classification Dagys (1972) unites those Carboniferous genera which in adulthood have entire hinge plates, free of the valve floor, other than for a connection by a median septum (see Fig. 171A–C). The dielasmatacean genera have hinge plates which join to the valve floor, tending to diverge anteromedially, leaving the middle of the valve floor free (Fig. 171D). Thus the Dagys (1972) classification seems to have merit and although amongst the Carboniferous genera the long-looped *Cryptonella* stands out from the rest in having about 450 endopuncta per mm^2 as compared to 100–250 per mm^2 in the short-looped forms, this characteristic may be more closely related to ecology than to supraspecific classification. Foster (1974) has shown that amongst living Antarctic brachiopods different species of the same genus may have varied punctal densities. He followed Campbell (1965) in suggesting that species from warm waters have more puncta per mm^2 than those from cold water, but also that greater depth may result in fewer puncta, despite the fact that warmer water occurred at depth in the Antarctic. The presence of different species in the Fermanagh samples with either high or low densities of puncta seems to contradict the idea that ecology is the most important factor controlling this feature and a full review of the punctal densities in terebratulids through time should be revealing.

In this faunal description I classify the species according to the work of Dagys (1972), which appears to be based on more sound principals than those of the *Treatise* (Williams *et al.* 1965). However, I use the terms for parts of the cardinalia more or less as in the *Treatise* and in Campbell (1965), as follows.

Outer hinge plates connect the crural bases to the inner socket ridges or valve floor laterally.

Inner hinge plates lie medially of the crural bases, meeting medially on a median septum, or fusing to the valve floor medially.

Crural bases are those parts of the crura fused with the hinge plates and separating outer from inner hinge plates.

Differences between the *Treatise* and Campbell's definitions occur when a median trough-like structure (as in *Girtyella*) is present. Campbell (1965) argued for a purely descriptive definition and called the structure a septalium, composed of the inner hinge plates only, while the *Treatise* (Williams *et al.* 1965) added the functional criterion of adductor muscle attachment, reserving the term septalium only for the structure not carrying adductor muscles. In the *Treatise* such a structure, with adductor muscle attachment, would be termed a cruralium. The problems of interpreting function make this *Treatise* definition undesirable.

Johnson & Westbroek (1971) discussed this problem of terminology, concluding that when cardinalia contained both subhorizontal and ascending plates (forming a V or Y to the valve floor) the terms inner hinge plates should be used for the former (subhorizontal structures) and crural plates for the latter. However, in terebratulids, where a double structure such as this is unknown, the distinction between crural bases or hinge plates remains problematical. It might be argued that the Y-shaped cardinalia of *Girtyella*, in section, are composed of crural plates converging to a median septum forming a septalium (*sensu* Johnson & Westbroek, 1971), or of inner hinge plates alone (*sensu* Campbell, 1965), or of inner hinge plates converging onto a median septum (*sensu* Williams *et al.*, 1965). The growth and role of the median septum is varied in terebratulides and I think it should not be critical to the use of the term septalium, which I restrict to the trough-like structure, supported or not by a median septum.

Superfamily **CRYPTONELLACEA** Thomson 1926

Family **CRYPTONELLIDAE** Thomson 1926

Genus ***CRYPTONELLA*** Hall 1861

REMARKS. Long-looped cryptonellids are seldom recorded from Carboniferous rocks of Europe, and the genus *Cryptonella* is externally similar to other short-looped genera such as *Cranaena* or *Dielasma*. If the loop is not preserved it can be difficult to distinguish long-looped species, but it may prove true that they are more densely endopunctate (*Cryptonella* having about 450 endopuncta per mm^2), and that their ventral umbones are straighter, having less incurved pedicle apertures in a submesothyrid position.

Cloud (1942) restricted the genus to the Devonian but Stehli, in the *Treatise* (Williams *et al.* 1965), extended it up into the Permian. The type species, *C. rectirostra* (Hall), comes from the mid-Devonian of North America. Several cryptonellid genera are recorded from the Permian of south-west Texas by Cooper & Grant (1976), but not *Cryptonella* itself.

Cryptonella minranensis sp. nov.

Figs 172–183

1982 *Cryptonella* sp.; Brunton: figs 2, 3.

DESCRIPTION. Small *Cryptonella*, commonly less than 10 mm long, with the greatest width at about two-thirds of the length. Anterior margin is rounded and the commissure rectimarginate. In lateral profile the shell is equibiconvex with prominent growth steps and a nearly straight to suberect pedicle umbo, the aperture being mesothyridid (Fig. 172a). Dental plates are well developed (Fig. 178a). In the dorsal valve the hinge plate is perforated posteriorly, remaining horizontal and unsupported between the inner socket ridges (Figs 177, 183). The crural bases extend across the hinge plate, close to the inner socket ridges, as both dorsal and ventral ridges. Endopunctation is dense and prominent, with about 450 endopuncta per mm^2.

NAME. From Minran Hill, 2 miles NNW of Derrygonnelly, Co. Fermanagh, adjacent to the type locality.

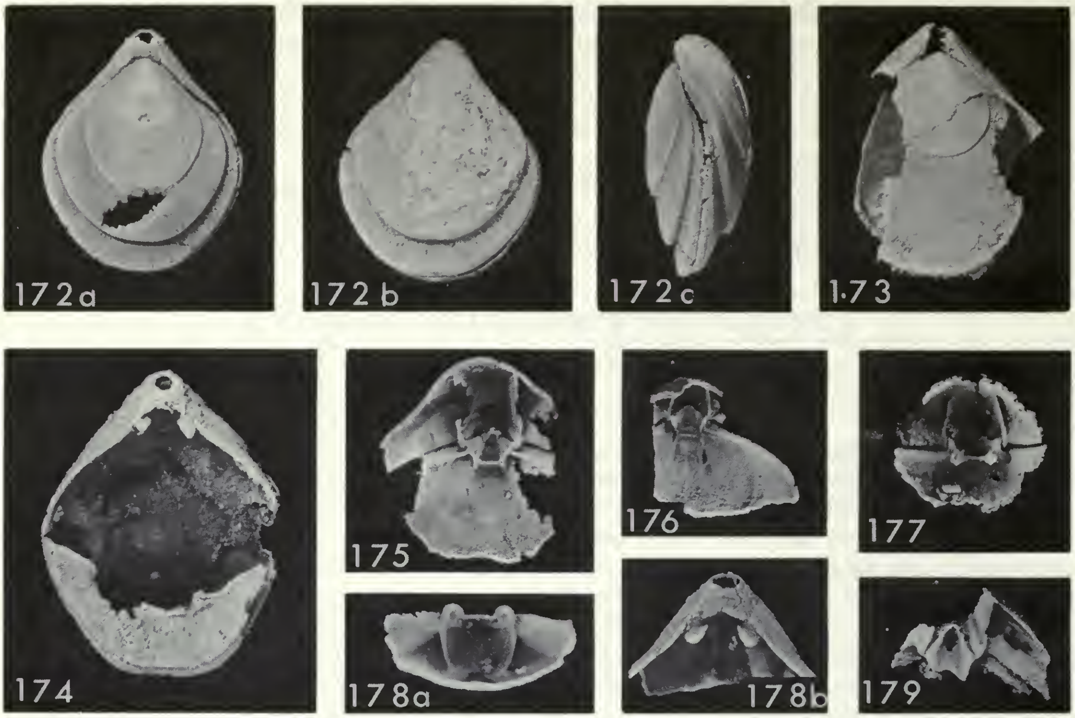
HOLOTYPE. BM(NH) specimen no BB64048; Fig. 172a–c.

LOCALITY. The type locality is collecting locality 14/4B, near Bunnahone Lough, Co. Fermanagh.

HORIZON. Asbian (D_1), Dinantian, Lower Carboniferous.

MATERIAL. About 140 specimens came from the type locality, 14/4B, below Minran Hill, near Bunnahone Lough: BB63166–BB63170, BB64030–BB64039, BB64048–BB64053, BD182–BD186. About 34 came from locality 14/4A at Carrick Lough: BB63986–BB63995, BB64023–BB64024. About 12 came from Milltown Bridge stream: BB63981–BB63985. Many of the specimens are fragmentary.

DISCUSSION. A diagnosis is not presented since other contemporary *Cryptonella* species are unknown. This is the most abundant of the four terebratulide species in the Fermanagh



Figs 172–179 *Cryptonella minranensis* sp. nov., from Co. Fermanagh. Fig. 172a–c, **holotype** viewed dorsally, ventrally and laterally; note the exposed deltidial plates and straight ventral umbo. BB64048, ×7. Fig. 173, dorsal view of incomplete shell (viewed stereoscopically in Fig. 180), from Carrick Lough. BB64023, ×8. Fig. 174, dorsal view of ventral valve showing the teeth. BB64049, ×6. Fig. 175, conjoined umbones viewed internally to show articulation, the cardinalia and crural bases (arrowed). BB64051, ×7. Fig. 176, conjoined umbones showing the cardinalia and crura. BB64052, ×2. Fig. 177, conjoined umbones viewed internally showing the articulation and unsupported hinge plates; from Carrick Lough. BB60024, ×10. Fig. 178a, b, ventral valve umbo viewed internally and dorsally showing the teeth and deltidial plates. BB64050, ×7. Fig. 179, internal view of a dorsal umbo, plus half the ventral umbo, showing the posteriorly perforate hinge plate. BB64053, ×7.

acid-developed faunas. The external shape can be confused most easily with *Girtyella carrickensis* sp. nov. (p. 110), but *C. minranensis* is relatively wider and has a suberect ventral umbo, leaving the deltidial plates exposed, as compared to the slightly incurved labiate beak of *G. carrickensis*. In addition the punctal density differs greatly; at about 450 puncta per mm^2 it is almost twice that of *G. carrickensis*. The dorsal valve cardinalia are quite different, but those of *Cryptonella* species are like those of *Alwynia* species, which can however be easily separated by the lack of dental plates, as in *A. reidi* sp. nov. (p. 114).

The strong development of growth halts, forming steps in the lateral profile of the shell, may not be characteristic of the species. The other three species also have some prominently-developed growth halts, so it is likely that these resulted from environmental factors rather than genetic control.

There are a few young specimens in the fauna in which brachial loops are preserved. These show that at a brachial valve length of about 4 mm there is an early cryptacanthiiform loop almost 3 mm long (Figs 180, 182). This juvenile loop has descending branches uniting anteromedially as an echmidium. At the median line of junction a vertical plate extends anteriorly, with a spinose serrated edge (Fig. 182b), and ventrally approaches close to the ventral valve. At this stage the ventral end of the median plate has a pair of lateral extensions

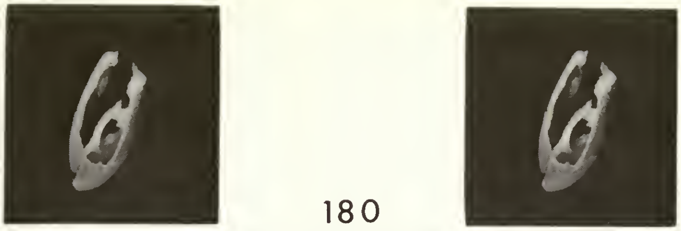
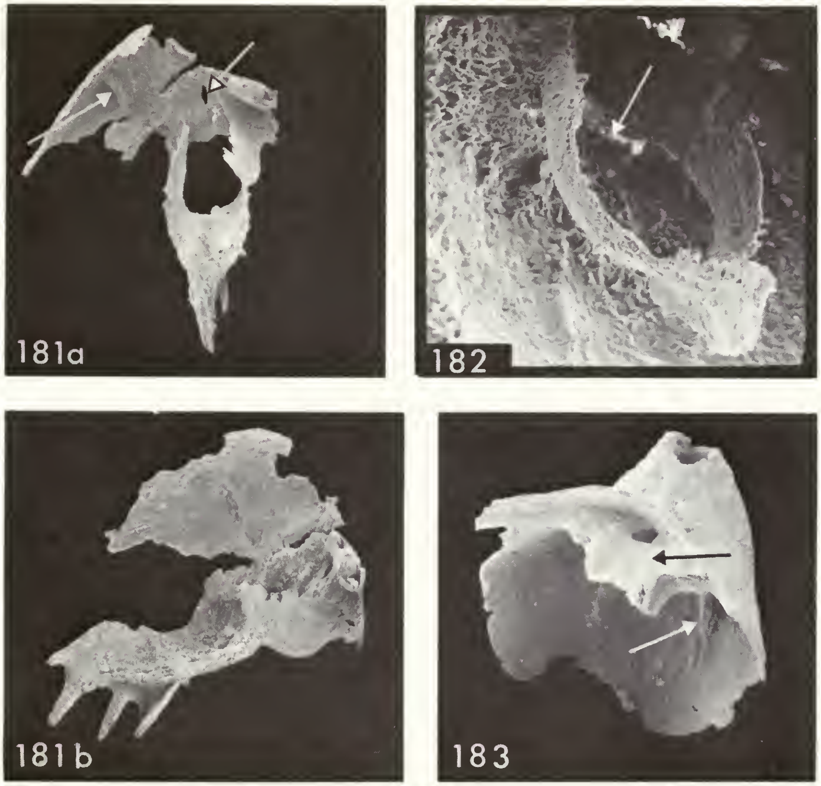


Fig. 180 *Cryptonella minranensis* sp. nov. Stereoscopic pair of an incomplete shell from Carrick Lough, viewed laterally to show the immature (cryptacanthiiform) brachial loop inside. BB64023, ×4; see also Fig. 173.



Figs 181–183 *Cryptonella minranensis* sp. nov., from Co. Fermanagh. Fig. 181a, b, brachial loop, with cardinalia and part of the ventral umbo, viewed ventrally and anterolaterally; one preserved dental plate and the hinge plate perforation are arrowed. BD182, S.E.M. ×15. Fig. 182, simple juvenile loop; the anterior edge of the hinge plate is arrowed. BD183, S.E.M. ×60. Fig. 183, conjoined umbones showing the underside of the perforate hinge plate, with ridges of the crural bases and one of the dental plates (both arrowed). BD184, S.E.M. ×15.

representing either an early stage in the development of the hood or the remnants of a broken hood. At this stage of development the loop is very similar to that described by Cooper & Grant (1976) in Permian Cryptonellidae.

Of the many terebratulide species described by de Koninck (1887) from the Carboniferous of Belgium, two externally resemble *Cryptonella* in appearing to have relatively straight to suberect ventral umbones. These are *Dielasma amygdaloides* de Koninck (1887: pl. 4, figs 26–40) and *D. subfusiforme* de Koninck (1887: pl. 5, figs 32–44). Of these, the former is somewhat more similar to *C. minranensis*, but without a knowledge of their interiors it is impossible to assign these de Koninck species accurately.

Family **CRANAENIDAE** Cloud 1942

Subfamily **GIRTYELLINAE** Stehli 1965

Genus ***GIRTYELLA*** Weller 1911

Weller first described the genus (1911: 442), with *Hattinia indianensis* Girty 1908 as type species. His sections of the type species clearly showed a concave hinge plate or septalium, supported from the umbo by a median septum. The *Treatise* (Williams *et al.* 1965) illustration (fig. 614.2b) is poor, showing the inner hinge plates as being too flat, while in fact they resemble more closely those of the Permian genus *Fletcherithyris* Campbell. Apart from any stratigraphical differentiation, *Girtyella* differs from *Fletcherithyris* in having a persistent dorsal median septum supporting the inner hinge plates, which, in *Fletcherithyris*, fuse to the valve floor and during growth anteriorly develop a median septum. Furthermore, Campbell (1965) points out that *Girtyella* has a medially-angled transverse band to its loop (lacking in his genus) and that the endopuncta of *Girtyella* have a density of about 280 per mm^2, as compared to 90 per mm^2 for *Fletcherithyris*.

Girtyella carrickensis sp. nov.

Figs 184–194

1982 *Girtyella* sp.; Brunton: fig. 4.

DIAGNOSIS. *Girtyella* widest at mid-length, with rounded anterior outline and rectimarginate commissure. Prominent ventral umbo with erect aperture. Inner hinge plates V-shaped both dorsally and anteriorly, supported by a low median septum extending anteriorly beyond the crural bases.

NAME. From Carrick Lough.

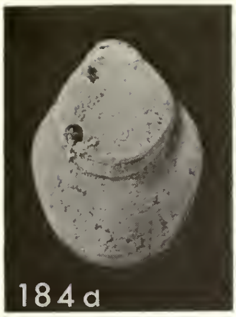
HOLOTYPE. BM(NH) specimen no. BB64000, Fig. 184a–c.

LOCALITY. The type locality is collection locality 14/4A at Carrick Lough, Co. Fermanagh, Ireland.

HORIZON. Probably early D_1, Asbian, Dinantian.

MATERIAL. About twelve specimens came from locality 14/4B (BB64025–BB64029, BB63033–63034), one hundred from the type locality 14/4A (BB64000–BB64009, BD186) and perhaps two specimens from the Milltown Bridge stream locality (BB63979), Co. Fermanagh. Thirty measured specimens range in length from 2·1 mm to 8·00 mm.

Figs 184–193 *Girtyella carrickensis* sp. nov., from Co. Fermanagh. Fig. 184a–c, **holotype** viewed ventrally, dorsally and laterally; the strong growth halt at about half the length is not a normal feature. From Carrick Lough. BB64000, ×3·75. Fig. 185a, b, young ventral valve interior and internal umbonal regions showing the teeth and dental plates. From Carrick Lough. BB64004, ×7. Fig. 186a, b, incomplete shell viewed laterally and dorsally. From Carrick Lough. BB64001, ×5. Fig. 187a, b, incomplete young dorsal valve viewed internally and tipped posteriorly, showing the crural bases (one arrowed) on the ventral surfaces of the hinge plates. From Carrick Lough. BB64005, ×7. Fig. 188, fragments of conjoined umbones viewed internally, showing the Y-shaped septalium, articulation and dental plates. From Carrick Lough. BB64003, ×5. Fig. 189, incompletely silicified conjoined umbones showing growth lines on the dental plate (arrowed). From Carrick Lough. BB64002, ×7. Fig. 190, dorsal valve interior, plus conjoined ventral valve umbo, with crura extending from the septalium. BB63033, ×6. Fig. 191, incomplete conjoined umbones; dorsal valve uppermost with the median septum (arrow 1) of the septalium supporting the hinge plates, upon which the crural bases (arrow 2) can be distinguished. The tooth (arrow 3) and a dental plate (arrow 4) are preserved. BD186, S.E.M. ×15. Fig. 192a, b, dorsal valve interior viewed dorsally and posterodorsally, showing the crura and a broken tooth in one socket (arrow). BB64026, ×7. Fig. 193a, b, incomplete dorsal valve interior viewed dorsally and posterodorsally showing the full septalium. BB64025, ×6.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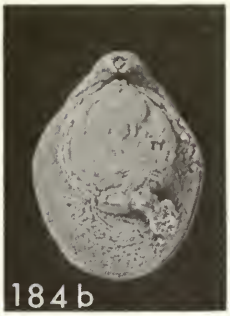
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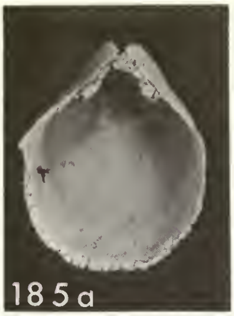
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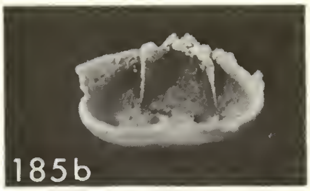
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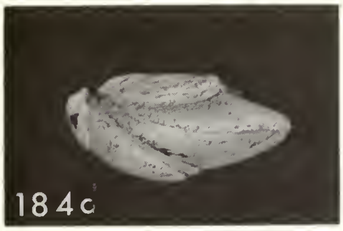
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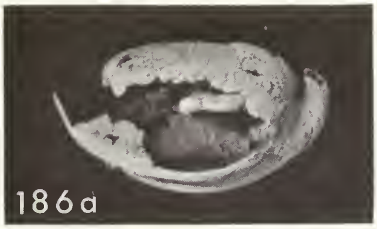
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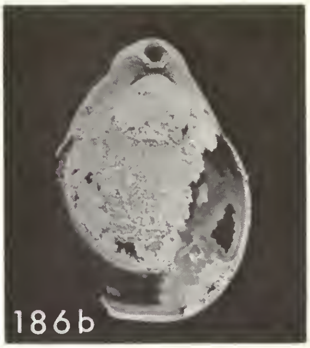
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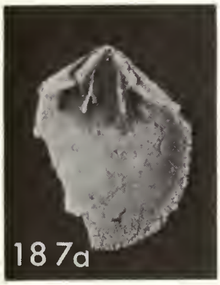
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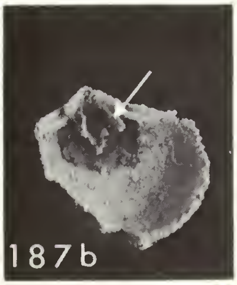
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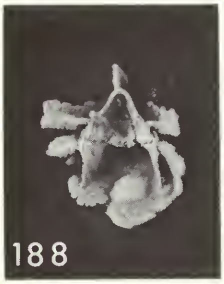
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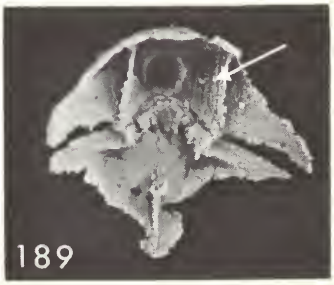
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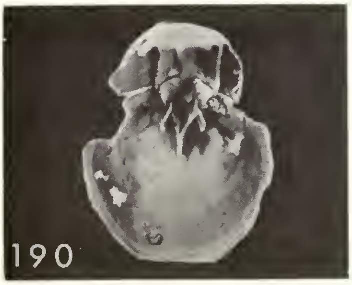
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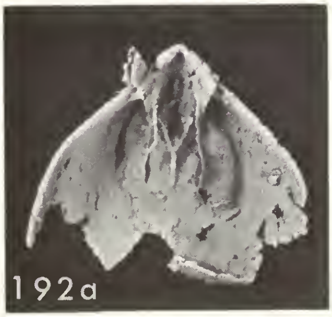
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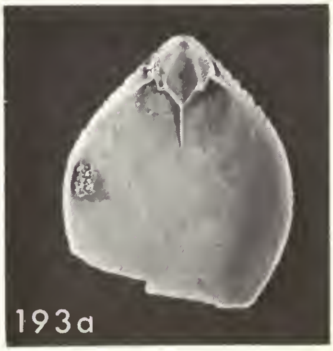
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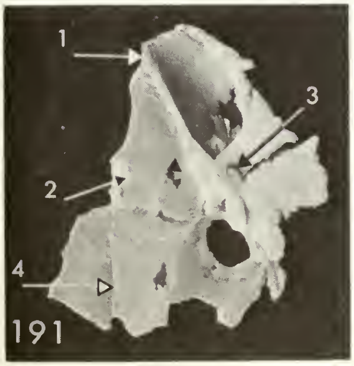

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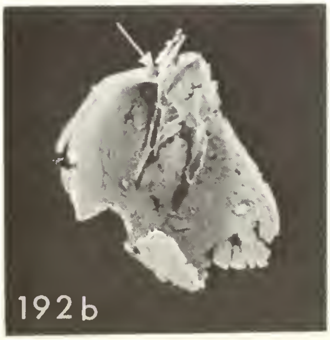
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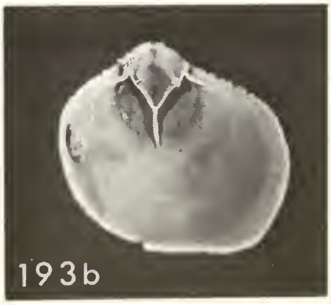
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Discussion. The hinge plates, characteristic of *Girtyella*, in this species look more like those depicted in the *Treatise* (Williams *et al.* 1965) for *Fletcherithyris* than for *Girtyella*. It should be noted that the *Girtyella* illustration (1965: fig. 614.2b) is inaccurate if compared with the original sections illustrated by Weller (1911, 1914) for *G. indianensis* (Girty), the type species. From Weller's description it is clear that the hinge plates should be somewhat V-shaped, being depressed medially (Fig. 193). The dorsal median septum in the Fermanagh material is persistent from the umbo (Fig. 188) and the average punctal density, taken from six specimens, is 240 endopuncta per mm^2, much greater than to be expected in species of *Fletcherithyris*.

Girtyella carrickensis has an internally thickened pedicle aperture (Fig. 189) which, in larger specimens, may have developed into a pedicle collar. The dental plates are well developed (Figs 189, 194). No specimen has an adult loop preserved, but the origins and dispositions of the crura can be seen (Fig. 192). Young specimens, about 5 mm long, retain a simple centronelliform loop (Fig. 194). Measurements from 30 complete specimens from the Carrick Lough locality show that the species retained fairly consistent dimensions, width being about four-fifths the length and the height of the shell being half the length. Specimens commonly have well-marked growth halts on their valves (Fig. 184), several of which are about 2 mm from the anterior margin. It may be, therefore, that an important local event took place affecting the population and inducing a major growth halt in shell deposition. In comparison with studied living Terebratulacea (G. B. Curry, personal communication 1969), this marginal 2 mm of shell since the growth halt would represent approximately six months' growth.

The ventral umbo of no specimen shows signs of abrasion, so it is concluded that the species had a relatively long pedicle for attachment, or that the substrate for their attachment was insufficiently hard to abrade the shell. As no specimen could be shown to be exactly *in situ*, with respect to its enclosing limestone, it is impossible to tell which was the more likely, but shell debris in the sediment could have provided sites of attachment.

G. carrickensis externally resembles de Koninck's (1887: pl. 7, figs 7–10) species *Dielasma avellana*, but as he gave no information about internal morphology it is impossible to make a generic assignment of his specimens.

Species of *Girtyella* have seldom been recorded from western Europe. Muir-Wood (1951) suggested that *T. sacculus* J. de C. Sowerby might belong to the genus, but I believe the species normally lacks dental plates and has *Dielasma*-like cardinalia, so it should be assigned to *Balanoconcha* Campbell, known from Viséan strata of eastern Australia.

Family **NOTOTHYRIDIDAE** Likharev 1960

Genus ***ALWYNIA*** Stehli 1961

Type species. *Terebratula vesicularis* de Koninck, 1851: 666; pl. LVI, figs 10; a rare species from the Visé district of Belgium. Lectotype selected by Brunton (1982) (Fig. 195).

Diagnosis (emended). Small Notothyrididae with anterior opposite or alternate folding. Puncta at about 200–250 per mm^2. No dental plates, small pedicle collar. Posteriorly perforate, unsupported cardinal plate.

Discussion. Stehli (1961) assigned only the type species to the genus, recording it from the Viséan of Britain and Belgium. His generic diagnosis included an antiplicate anterior commissure, being the form of *A. vesicularis*. I treat this as a specific characteristic, broadening the generic diagnosis to include species having different commissural types, such as the rectimarginate, ligate form of *A. reidi* sp. nov. Judged from ten specimens of *A. vesicularis* (de Koninck) in the de Koninck collection of the British Museum (Natural History), it seems that the original figures of the species by de Koninck (1851: pl. 56, figs 10a–d) are uncharacteristic. These figures are of a species almost as wide as long, whereas nine of the ten specimens are consistently 2 to 3 mm longer than wide, at lengths of about 13 mm. The specimen from the Isle of Man illustrated by Stehli (1961: pl. 62, figs F1–5) is comparable to the de Koninck specimens, but differs in being slightly more strongly antiplicate and in having a slightly flatter dorsal valve.

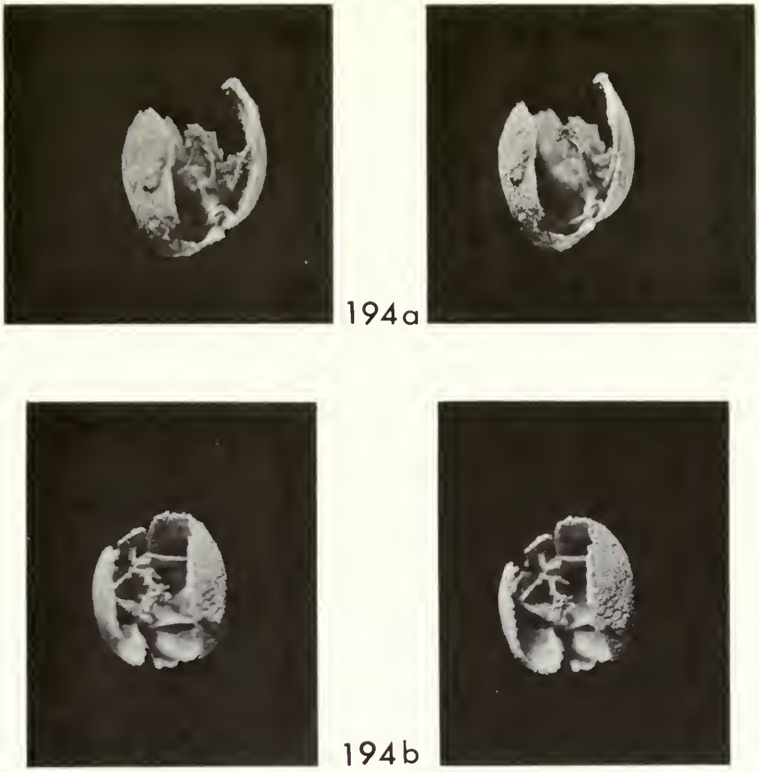


Fig. 194 *Girtyella carrickensis* sp. nov. from Carrick Lough, Co. Fermanagh; stereoscopic pairs. a, viewed posterolaterally, showing the brachial loop and articulation. b, viewed posteriorly, showing the loop in relation to the cardinalia. BB64006, ×6.

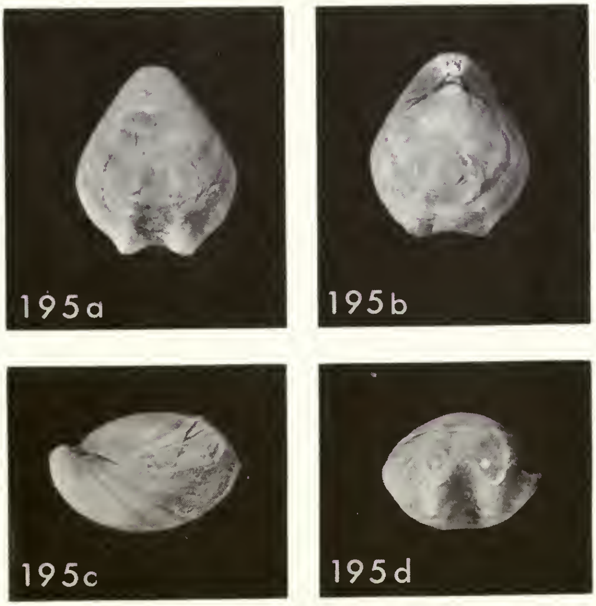


Fig. 195 *Alwynia vesicularis* (de Koninck) from the Viséan of Visé, Belgium; selected as lectotype by Brunton (1982). Ventral, dorsal, lateral and anterior views. BD80, ×2·5.

Alwynia reidi sp. nov.
Figs 196–199

1982 *Alwynia* sp.; Brunton: fig. 11.

DIAGNOSIS. Small (less than 10 mm long) *Alwynia* with rectimarginate anterior commissure and slight opposite folding, creating a ligate outline. Crural bases form ridges on dorsal surface of the hinge plate.

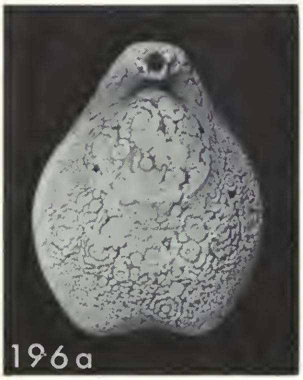
NAME. After R. E. H. Reid of Queens University, Belfast, who first acid-etched faunas from the type locality.

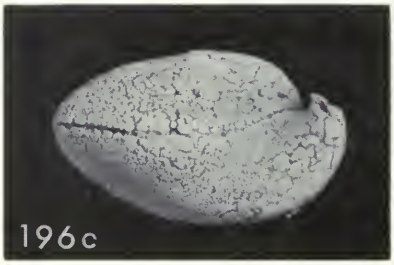
HOLOTYPE. BM(NH) specimen no. BB64046, Fig. 196a–c.

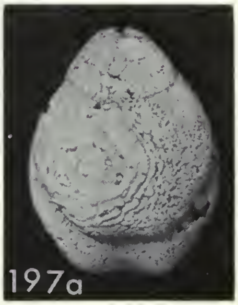
LOCALITY. Collecting locality 14/4B, near Bunnahone Lough, Co. Fermanagh.

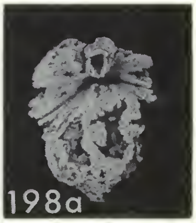
HORIZON. The age of the limestones yielding the type specimen is thought to be early Asbian (D_1), Viséan.

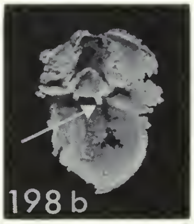
MATERIAL. Ten specimens, mostly incomplete, came from the Carrick Lough locality (BB64010–BB64022); eight, including the holotype (Fig. 196a–c), from the Bunnahone locality (BB64046–BB64047, BD109–BD113); and about three incomplete specimens from the Milltown Bridge Stream locality (BB63980). All in Co. Fermanagh.

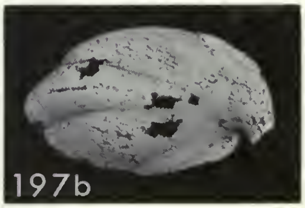


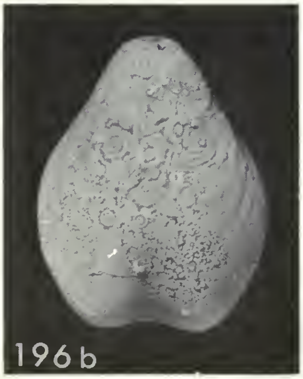


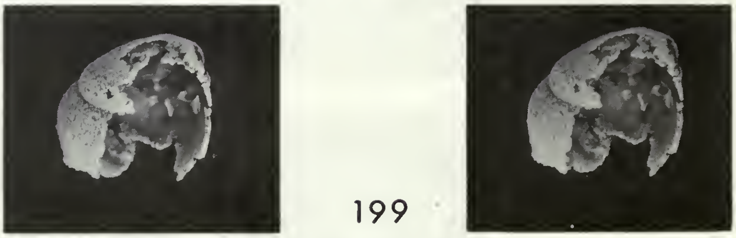












Figs 196–199 *Alwynia reidi* sp. nov., from Co. Fermanagh. Fig. 196a–c, **holotype** viewed dorsally, laterally and ventrally. BB64046, ×4·5. Fig. 197a, b, shell from Carrick Lough viewed ventrally and laterally. BB64020, ×5. Fig. 198a, b, conjoined umbones viewed externally and internally, showing crural bases (arrowed) extending from the hinge plate. From Carrick Lough. BB64022, ×6. Fig. 199, stereoscopic pair of incomplete shell viewed posteriorly, showing the crura. From Carrick Lough. BB64021, ×4.

Description. Small *Alwynia* with equibiconvex lateral profile, rectimarginate anterior commissure and a ligate outline. The ventral valve sulcus developed from a length of about 5 mm (Fig. 196b). Internally, the pedicle collar is most fully developed ventrally. In the cardinalia the inner socket ridges are strong and in plan view form a rounded V-shaped structure by posterior fusion near the indistinct cardinal process (Fig. 198b). The sockets are supported by lateral shell thickening and the unsupported median hinge plate has a small posterior perforation.

Discussion. In the past virtually any dielasmatacean with a folded ventral valve, from the Dinantian, was called *Dielasma sacculus* (J. de C. Sowerby), and at first I thought this was the taxon for the Fermanagh species. Externally the shapes of the two species are similar, although Sowerby's species has a uniplicate anterior commissure and its widest part is nearer the front than in *A. reidi*. The clear difference, however, is internal; the inner hinge plates of *Terebratula sacculus* form an open V to the valve floor, in a fashion characteristic of *Balanoconcha*, while in *A. reidi* the hinge plate is horizontal and unsupported between the inner socket ridges (Figs 198b, 199). The new species differs from *A. vesicularis*, the type species, in lacking the anteriorly-developed plications on the ventral valve which contribute to the antiplicate anterior commissure (Fig. 195a, b). Judged from Stehli's (1961) serial sections and drawing, the cardinalia are very similar, indeed the more so from his sections than from the drawing which, incorrectly, shows the crural bases forming ridges along the ventral surface of the hinge plate.

Two of de Koninck's 1887 'species' look externally similar to *A. reidi*, one called *Dielasma finale* (1887: 24), the other *D. gemmula* (1887: 29). The second is the more similar and, if the specimens exist and prove to belong to *Alwynia*, it might be conspecific with the Fermanagh species. *D. gemmula* came from late Viséan rocks of the Visé region, Belgium.

Superfamily **DIELASMATACEA** Schuchert 1913

Family **DIELASMATIDAE** Schuchert 1913

Genus ***BALANOCONCHA*** Campbell 1957

Type species. *B. elliptica* Campbell, 1957, from the Watts district of New South Wales, Australia. Originally it was dated as being of Tournaisian age, but more recent revisions of the stratigraphy of eastern Australia assign the rocks to zones 4 to 6, correlating with mid to upper Viséan of Europe.

Discussion. The genus is included here, despite not occurring in the Fermanagh faunas, because it was thought initially that one of the species may have belonged within *Balanoconcha*, and investigations demonstrated for the first time that the genus exists in Britain.

Alwynia reidi sp. nov. (p. 114) externally somewhat resembles the species *Terebratula sacculus* J. de C. Sowerby, so it was important to find the genus to which this species belonged. Muir-Wood (1951) selected a Sowerby specimen, BM(NH) no. B61653, as lectotype; writing that it had a single dental plate and a dorsal median septum, she suggested that it be assigned to *Girtyella*.

A re-examination of the lectotype of *T. sacculus* (see Brunton 1982: fig. 14) leads me to believe that it had only one 'plate' (perhaps a pathological structure or even a piece of shelly debris, such as part of the loop, lodged in the umbo) in the ventral valve. The serial sectioning of three specimens from Narrowdale, Staffordshire, within a few miles of the Derbyshire localities given for *T. sacculus*, shows that the normal condition of the species is to lack dental plates. Furthermore, the cardinalia are not Y-shaped in transverse section, as are those of *Girtyella*, but somewhat V-shaped, with the V opening anterodorsally as in *Balanoconcha*.

Terebratula sacculus J. de C. Sowerby should, therefore, be assigned to *Balanoconcha*. There is a second species, from late Viséan rocks in Britain, which was called *sacculus* and figured by Sowerby (1824: pl. 446, fig. 1) on the same plate as the lectotype of *B. sacculus*, but this is smaller and much more strongly folded. It belongs to the genus *Harttella* Bell, 1929, and is described in my general review of British Dinantian terebratulides (Brunton 1982: 50).

Family **HETERALASMINIDAE** Likharev 1956

Genus ***BEECHERIA*** Hall & Clarke 1894

Type species. *B. davidsoni* Hall & Clarke, 1893.

Discussion. The genus was first separated from *Dielasma* in the mistaken belief that it was devoid of dental plates. In his fine study of the Windsor Group faunas Bell (1929) discovered dental plates in the type species, *B. davidsoni*, and assigned it to *Dielasma*; at that time the significance of the different cardinalia had not been recognized. It was this difference that Stehli (1956) used in reviving *Beecheria*, but as pointed out by Campbell (1965), Stehli's sections, purporting to be of *Beecheria*, do not seem to be of the type species from the Windsor Group of Nova Scotia. Campbell (1965: 53) obtained specimens from there and produced serial sections which are probably a truer representatoin of the species, and genus. They match the Fermanagh material and show that the dorsal valve umbo does not have a short median septum (as on Stehli's sections), but that once the hinge plates lose contact with the inner socket ridges they continued to grow anteriorly as a diverging pair of inverted V-shaped ridges. Furthermore Campbell (1965) showed that the median segments of the hinge plates unite as a delicate

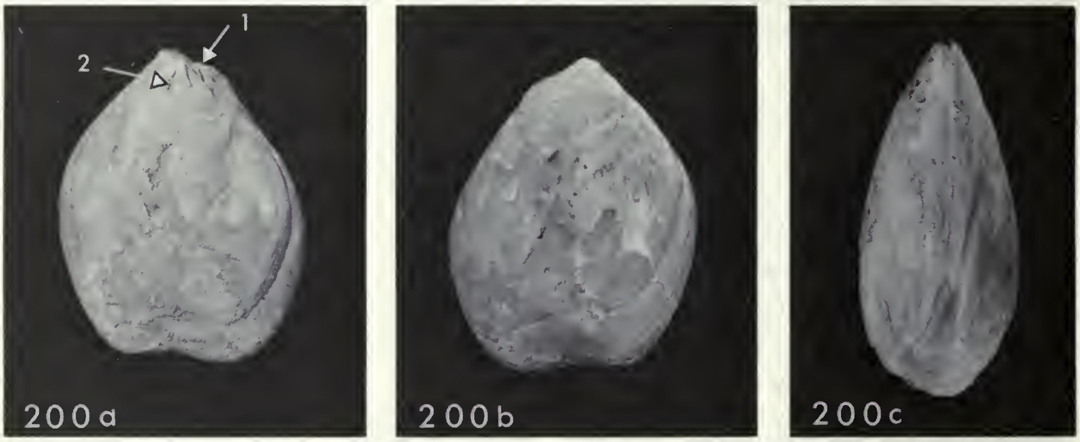
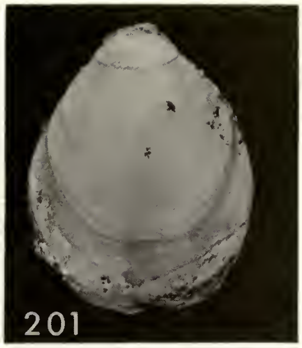


Fig. 200 *Beecheria hastata* (J. de C. Sowerby). Lectotype selected by Parkinson (1952), viewed dorsally, ventrally and laterally. Arrow 1 points to a dental plate and arrow 2 to the impression of the posterior ends of the hinge plates. From the early Viséan of Limerick, Ireland. B61657, ×1.

Figs 201–210 *Beecheria treakensis* sp. nov. Figs 201–207 from Co. Fermanagh, Figs 208–210 from Treak Cliff, Derbyshire. Fig. 201, ventral valve exterior. BB64040, ×2. Fig. 202a, b, part of dorsal valve viewed dorsally and anteriorly, showing the cardinalia and ventrally disposed crura. BB64044, ×8. Fig. 203a, b, incomplete dorsal valve interior viewed laterally and posteriorly; the cardinal process is arrowed and the inverted V-shaped hinge plates are clearly seen, including the crural base (arrowed). BD181, S.E.M. ×10. Fig. 204, incomplete dorsal valve interior with a fragment of ventral valve attached at one tooth. BB64042, ×2·5. Fig. 205, cardinalia of adult dorsal valve showing the cardinal process and sessile median septalium. BB64043, ×5. Fig. 206, part of dorsal valve interior showing one elongate socket, outer hinge plate and part of the median septalium (arrowed). BB64045, ×3. Fig. 207, incomplete ventral valve exterior viewed anteroventrally, to display the small teeth (arrow) and the labiate pedicle opening. BB64041, ×4. Fig. 208a, b, internal mould of specimen from Treak Cliff. a, dorsal view with the positions of dental plates showing (arrowed), ×1. b, oblique view showing the impressions of the hinge plates (arrow 1) and median septum of the septalium (arrow 2), ×2. BD3. Fig. 209, anterior end of dorsal valve from Treak Cliff, displaying radial 'colour' banding. BD4, ×2. Fig. 210a–e, **holotype** seen posteriorly, anteriorly, dorsally, ventrally and laterally; most of the shell is missing allowing the dental plates (arrowed) to show, as well as traces of the cardinalia in Fig. 210c. From Treak Cliff. BD1, ×1·5.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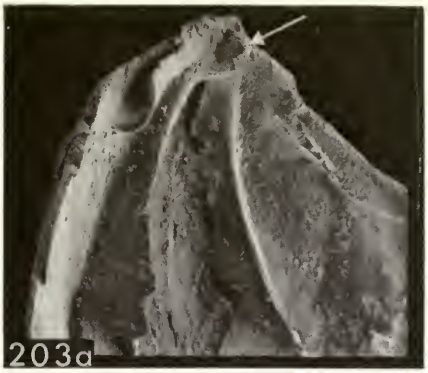
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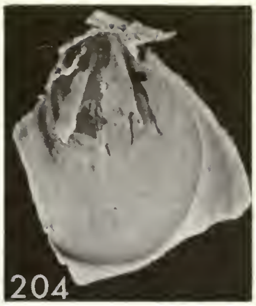
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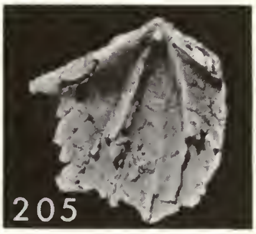
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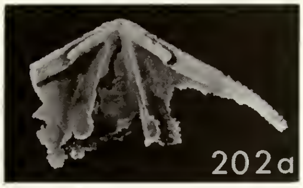
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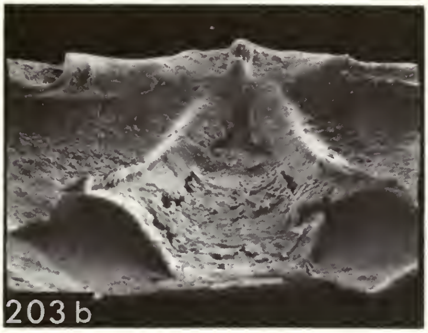
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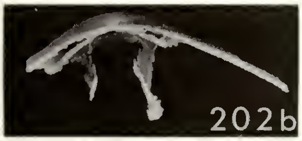
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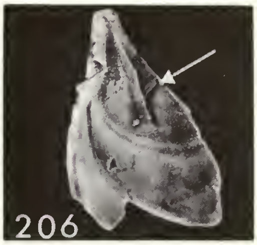
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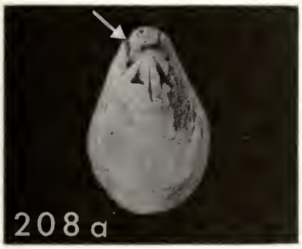
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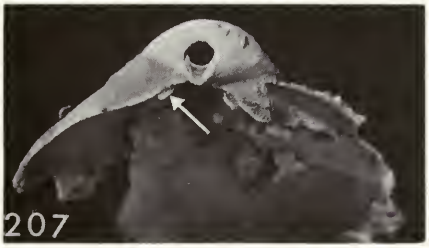
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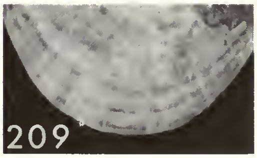
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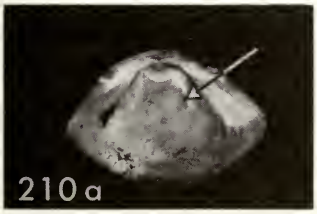
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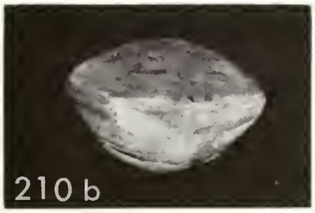
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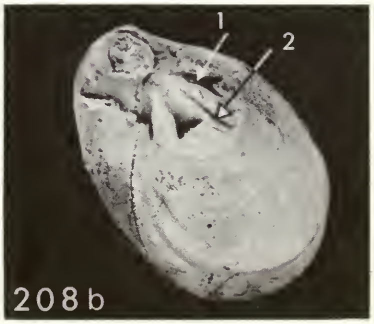

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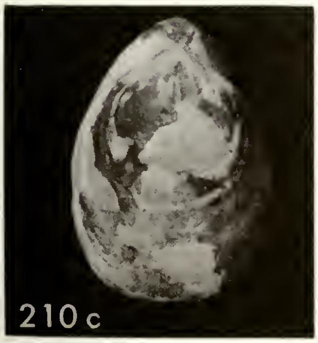
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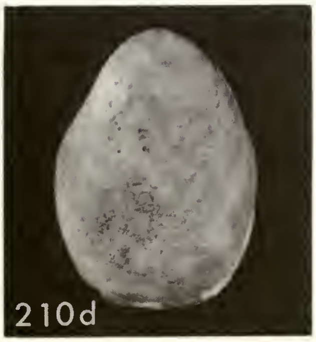
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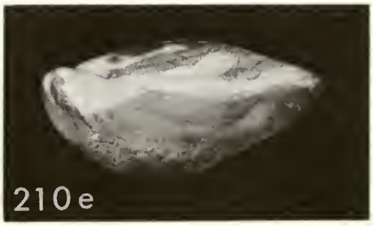

210e

septalium very close to the valve floor. This structure is repeated in the Fermanagh species (Fig. 205). Campbell assigned several dielasmid species, described by Weller (1914) from the Mississippi Valley, to *Beecheria*, including *B. arkansana* (Weller) which is similar to the Fermanagh species, although not conspecific.

Species of *Beecheria* have not previously been recorded from western Europe, although some of the species assigned to *Dielasma* by de Koninck (1887) should belong here (e.g. *D. tumidum* de Koninck). However, in my brief review of British Dinantian terebratulide genera (Brunton 1982: 53) I discussed the status of *Beecheria* and illustrated the interior of the true *B. hastata* species (Fig. 200) from a set of serial sections reproduced in their correct orientations by a computer program (1982: fig. 20). Those illustrations showed an interior closely comparable to the interiors seen in the Fermanagh silicified material.

Beecheria treakensis sp. nov.

Figs 201–211

?1887 *Dielasma tumidum* de Koninck: 12; pl. 2, figs 27–29.
?p.1887 *Dielasma avellana* de Koninck: 22; pl. 7, figs 7–10.
?p.1887 *Dielasma radiatum* de Koninck: 24; pl. 7, figs 39, 40.
?p.1887 *Dielasma itaitubense* (Derby) de Koninck: 26; pl. 5, figs 1–10.
v. 1952 *Dielasma hastata* (J. de C. Sowerby) Parkinson: text-fig. 1, nos. 1, 2.
1982 *Beecheria* sp.; Brunton: figs 15, 18, 19.

DIAGNOSIS. Medium length (seldom more than 30 mm) *Beecheria* with approximately ovate outline and flattened dorsal valve, seen in lateral profile. Anterior margin smoothly rounded, with rectimarginate commissure.

HOLOTYPE. BM(NH) specimen no. BD1, from Treak Cliff, near Castleton, Derbyshire, collected by D. Ward. Fig. 210a–e.

HORIZON. The 'Brachiopod Beds', Lower Carboniferous, Asbian age (D_1).

MATERIAL. Twenty-three paratypes in the Ward collection (BD2–BD18). The species is not common in the Fermanagh faunas but thirteen specimens were recovered from the Sillees River locality (BB64040–BB64045) and eight from Carrick Lough (BB63996–BB63999); all the silicified specimens are fragmentary.

DESCRIPTION. These elongate *Beecheria* specimens vary somewhat in outline but their dorsal valves, especially over the umbones, are characteristically flat (Fig. 210e). The anterior margin is normally gently rounded, but rarely is almost straight. Only very rarely is the commissure slightly uniplicate. The ventral umbo is prominent, with a labiate (Fig. 207), dorsally-directed aperture. Radial colour banding may be preserved (Fig. 209).

Dental plates are short, being confined to the umbo, and in posterior view diverge only slightly (Fig. 210a). Adults have a small knob-like cardinal process (Figs 203b, 205) at the posterior apex of paired diverging hinge plates forming inverted Vs on the valve floor (Fig. 203) and, medially, a very low septalium bearing concentrically-ridged muscle scars separated by a low myophragm (Fig. 205). The sockets are elongate, at the valve margin, and unsupported. The density of endopuncta is approximately 90 to 120 per mm^2.

DISCUSSION. Exfoliation of the shell on some Treak Cliff specimen displays the short dental plates and fine shelly ridges in the dorsal valve typical of the *Beecheria* cardinalia (Fig. 208a, b). These structures are well seen in the Irish silicified material (Figs 202–205), from which it is also clear that the outer plates are stronger than the inner and give rise directly to the crura. As the crura separate from their bases they form ventrally slightly divergent and deep shelly portions of the posterior loop (Fig. 202); however, the full loop is not preserved in this material.

B. treakensis resembles the type species, *B. davidsoni*, in several internal characteristics, including the general form of the crura and their bases. Bell (1929) described the rudimentary dorsal median septum and plate for muscle attachment between the crural bases, such as is seen well on some Fermanagh specimens (Figs 204, 205). *B. davidsoni*, according to the illustrations provided by Bell (1929: pl. 23, figs 8–10, 15–18), which include the lectotype, is a fatter species, having a more normally convex dorsal valve, as seen in lateral profile. The two species are, however, closely related and this is not surprising since *B. davidsoni* comes from the Windsor Group of Nova Scotia, commonly correlated with mid to upper Viséan rocks of Europe. Bell's commonest occurrence of *B. davidsoni* is recorded as his B and C levels of the Windsor Group and he correlated the junction between these levels as at the start of the British D Zone, the Asbian. Thus the species appears to correlate with late Holkerian to early Asbian, close to the age of the Fermanagh fauna. Brunton & Mason (1979) commented on the relationships of Fermanagh sabkha-like Meenymore rocks to those of eastern Canada and the likelihood of the two areas having been closer in Carboniferous times than today. However, Jansa, Mamet & Roux (1978) concluded that the microfaunas of the two regions precluded a close geographical relationship and suggested the existence of a 'deep ocean or sea (that) separated Ireland from eastern Canada during the Viséan' (1978: 1428). Since several of the brachiopods described by

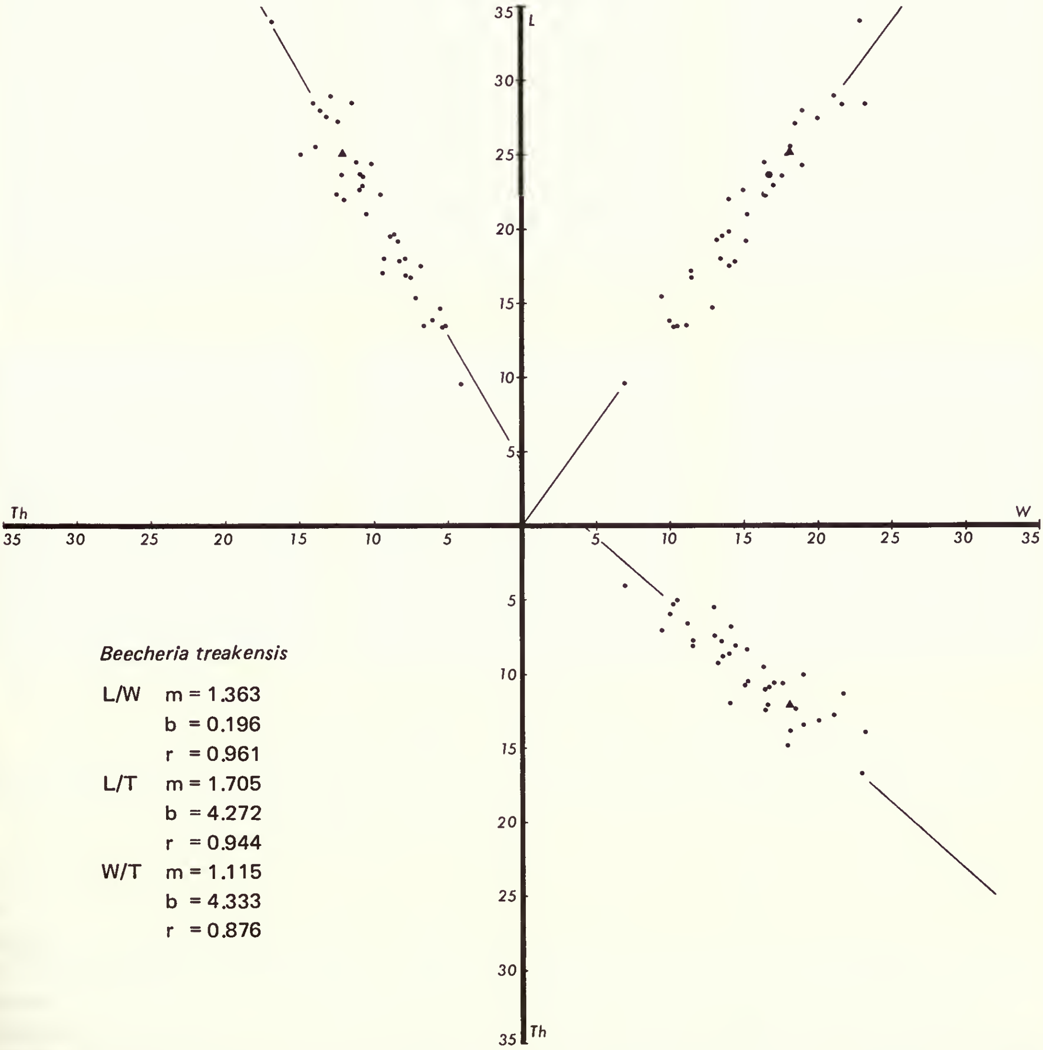


Fig. 211 *Beecheria treakensis* sp. nov. Length, width and thickness plots of 38 specimens from Treak Cliff, Derbyshire; holotype = ▲. m = slope of regression line; b = intersection point of m with axis; r = coefficient of correlation.

Bell (1929) from the Windsor Group resemble European Viséan species morphologically, it seems that we have something of a conflict. The late Viséan evaporitic deposits may have accumulated on opposite sides of a deep sea, which stopped benthonic microfaunal migration, but which developed only early in the Viséan, allowing some brachiopods to flourish on both shelves while retaining similar morphologies. Certainly by Namurian times the brachiopods were diverging, to become increasingly European or North American in character.

Beecheria species in the European Carboniferous are probably relatively common. The possible de Koninck (1887) synonyms include some specimens which undoubtedly are *Beecheria* species (e.g. *B. tumidum*), but the information on these Belgian specimens is insufficient to allow sure synonymy. In addition most of de Koninck's species names have not been reused and so should be considered as forgotten names (*nomina oblita*). For these reasons, and the lack of precision in their localities and horizons, I have not resurrected a de Koninck species name. *Beecheria hastata* (J. de C. Sowerby) is the common species in earlier Viséan rocks, the type specimen coming from probable Arundian rocks of the Limerick area of Ireland (Fig. 200a–c). The previous 'sack' use of *Dielasma hastata* has included specimens of *B. treakensis*, as, for instance, the two largest specimens of the series drawn in outline by Parkinson (1952) (but note that he exaggerated the uniplication in his second specimen, BM(NH) no. BB14869, attributed here to *B. treakensis*). Most of his other specimens are *Balanoconcha sacculus* (J. de C. Sowerby); none is *B. hastata*! It seems probable that serial sectioning or dissection to reveal the cardinalia of several European Carboniferous terebratulides will result in emendations of their generic assignments. Both *Dielasma* and *Beecheria* have dental plates, but it is generally easy to distinguish dorsal valves from which the shell has exfoliated posteriorly: *Dielasma* shows only the two traces of the inner hinge plates against the valve floor, whilst *Beecheria* displays the four traces of both the outer and inner hinge plates, with connections to the inner socket ridges only in the apex of the umbo. The diversity of *Beecheria* may prove greatest in the Carboniferous and of *Dielasma* in the Permian.

Appendix 1

The development of samples from the Sillees river locality since the publication of my paper on the productoids (1966*a*) has revealed seven examples of an additional species, briefly described below since interiors can be seen for the first time.

Family **MARGINIFERIDAE** Stehli 1954

Genus ***EOMARGINIFERA*** Muir-Wood 1930

Eomarginifera derbiensis (Muir-Wood)

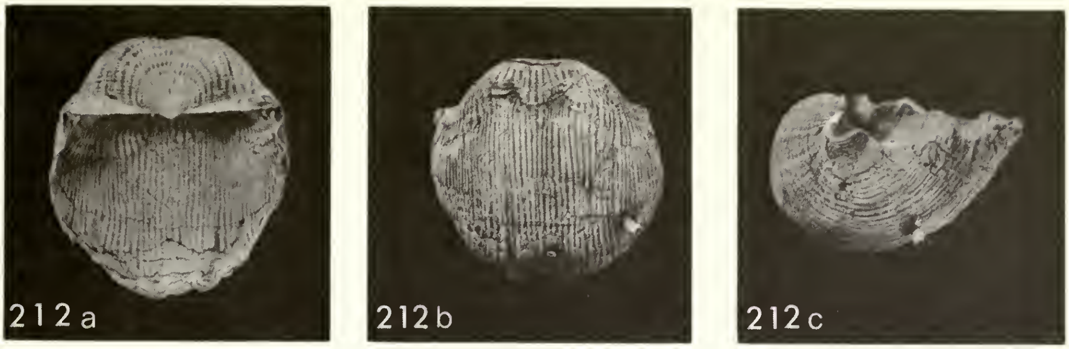
Figs 212–213

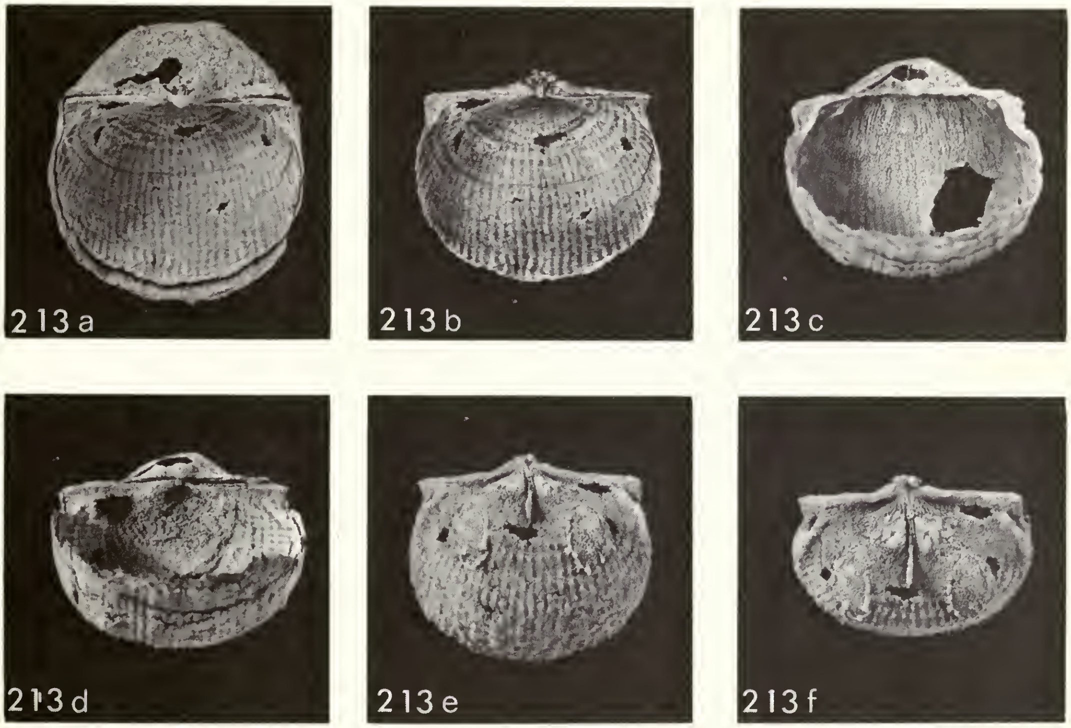
v* 1928 *Productus derbiensis* Muir-Wood: 170; pl. 11, figs 10, 11, 19a–c.

DIAGNOSIS. Medium to large eomarginiferids with rounded, non-geniculate, lateral profile and no median sulcus. Close, well-defined, ribbing (about 9 in 5 mm width at 10 mm from ventral umbo), with accentuated ribs on flanks by strongly differentiated small ears.

HOLOTYPE. BM(NH) specimen no. B43730, from Thorpe Cloud, Derbyshire (Muir-Wood 1928: pl. 11, fig. 10).

DISCUSSION. In 1928 Muir-Wood figured two specimens as *P. derbiensis*, the holotype and a second from Wetton, Staffordshire, BM(NH) no. B45516, which she called a 'Giganteid Form' (pl. 11, figs 19a–c). The maximum width of the holotype is 18·6 mm, while this large specimen is 25·5 mm wide. Because of its greater size this Wetton specimen has more major spines than the holotype, with an extra pair and a median spine on the ventral venter. The Fermanagh specimens display a similar range in size with one complete ventral valve at 16·9 mm maximum width, one at 21·2 mm (Fig. 212) and the largest at about 29·5 mm (one ear is missing). Again,





Figs 212–213 *Eomarginifera derbiensis* (Muir-Wood) from the Sillees river, Co. Fermanagh. Fig. 212a–c, posterodorsal, ventral and lateral views of a complete shell. BB64648, ×1·5. Fig. 213a–f, complete shell. a, posterodorsal view of complete shell. b, posterodorsal view of dorsal valve alone, showing the cardinal process. c, interior view of ventral valve, showing the anterior ends of the diductor muscle scars. d, anterodorsal view of complete shell. e, internal view of dorsal valve. f, internal view of posterior region. BB64649, ×2.

while details of the spine patterns anterior of the rugose areas differ, in other respects the specimens seem conspecific.

In her original description Muir-Wood was unable to describe the shell interior, but the Fermanagh material includes some complete disarticulated valves displaying their internal morphologies (Fig. 213c, e, f). This is typically marginiferid in its broad, sessile cardinal process, anteriorly high breviseptum, raised dorsal adductor scars, clear brachial ridges and shelly ridges across the ears. However, no anterior marginal ridge appears to have developed (Fig. 213e).

Muir-Wood's original (1928) wide stratigraphical range for the species was later (Muir-Wood

& Cooper 1960) restricted to the Viséan, but I think the range should be further restricted to mid and upper Viséan, especially the Asbian and Brigantian stages.

Eomarginifera derbiensis differs from *E. lobata* (J. de C. Sowerby) or *E. setosa* (Phillips) in its finer ribbing and lack of median sulcation.

Appendix 2: List of brachiopod species

The full list of brachiopods recognized from the two localities (on the Sillees river and at Carrick Lough, Fig. 1, p. 29) is given below. An indication of the relative abundance of the various species is provided: a very rare (vr) species has fewer than five individuals; a rare (r) species between 6 and 20 individuals; a species is termed present (p) if represented by 21–50 individuals; common (c) if between 51 and 100 individuals, and abundant (a) if over 100 individuals. In addition '+' indicates high numbers in the category, and '−' indicates low in the category. The counts were based upon estimates of complete specimens, ignoring the numerous fragments of valves.

Described in 1968 (Brunton 1968):

Crania quadrata (M'Coy)	r
Acanthocrania cf. *laevis* (Keyes)*	r
Philhedra trigonalis (M'Coy)	r
Schizophoria resupinata dorsosinuata Demanet	p+
Rhipidomella michelini (Léveillé)	c+
Leptagonia analoga (Phillips)	r+
Brochocarina wexfordensis (Smyth)*	p
Orthotetinid [*Apsocalymma* MacKintosh 1974]	vr
Serratocrista fistulosa Brunton	p
Schellwienella radialis (Phillips)*	r
Globosochonetes parseptus Brunton*	a+
Rugosochonetes silleesi Brunton*	a
Rugosochonetes delicatus Brunton*	r+
Rugosochonetes transversalis Brunton*	r
Plicochonetes buchianus (de Koninck)	r

Described in 1966 (Brunton 1966*a*):

Heteralosia cf. *fortispinosa* (Hinchey & Ray)	c−
Dasyalosia panicula Brunton*	c+
Dasyalosia lamnula Brunton	c+
Acanthoplecta mesoloba (Phillips)	r
Plicatifera plicatilis (J. de C. Sowerby)	p
Productina margaritacea (Phillips)	c+
Overtonia fimbriata (J. de C. Sowerby)	c−
Avonia (Quasiavonia) aculeata (J. de C. Sowerby)	c+
Krotovia spinulosa (J. Sowerby)*	a+
Krotovia lamellosa Brunton*	a−
Eomarginiferina trispina Brunton*	a+
Echinoconchus cf. *punctatus* (J. Sowerby)	r−
Pustula cf. *pyxidiformis* (de Koninck)	vr
Antiquatonia sp.	r
Ovatia sp.	vr
Chonopectinid [description in preparation]	vr
Eomarginifera derbiensis (Muir-Wood) [see p. 120]	p

Herein:

Propriopugnus pugnus (Martin)	vr
Pleuropugnoides pleurodon (Phillips)	r
Tretorhynchia trilatera (de Koninck)	p+
Coledium seminulum (Phillips)	r
Hustedia radialis (Phillips)	a+
Hustedia ulothrix (de Koninck)	r

Actinoconchus lamellosus (Léveillé)	r
Cleiothyridina fimbriata (Phillips)*	c+
Cleiothyridina deroissei (Léveillé)	p+
Crurithyris urei (Fleming)	a+
Nucleospira carlukensis (Davidson)	p+
Cyrtina hibernica sp. nov.*	a+
Tylothyris laminosa (M'Coy)*	p
Fusella rhomboidea (Phillips)	r
Skelidorygma integricosta (Phillips)	vr
Spiriferellina insculpta (Phillips)	c+
Merospirifer linguifera (Phillips)	vr
Phricodothyris verecunda George	p−
Minythyra lopha sp. nov.	r+
Minythyra ernea sp. nov.	p−
Cryptonella minranensis sp. nov.*	c
Girtyella carrickensis sp. nov.*	c
Alwynia reidi sp. nov.*	r
Beecheria treakensis sp. nov.	r

A small collection of silicified specimens was developed from a limestone, lower in the Glencar Limestone, which crops out in the stream draining east from the Black Slee forest area to Lower Lough Erne at Holme Bay. The locality is about 610 m south-west from Milltown Bridge and about 1465 m WNW of Church Hill, near Derrygonnelly, Co. Fermanagh. Seventeen of the above species (*) were recognized in this *Schellwienella*-rich argillaceous limestone. In the text this locality is termed Milltown Bridge Stream.

Acknowledgements

I thank Sir Alwyn Williams, F.R.S., for the facilities placed at my disposal while he was Head of the Department of Geology, Queen's University, Belfast, where the collecting and acid development of the faunas here described were carried out. Thanks are due to the following for the loan of specimens in their care: G. A. Cooper of the National Museum of Natural History, Washington, U.S.A.; the late J. M. Edmonds and W. J. Kennedy of the University Museum, Oxford; Mme D. Gaspard of the Université de Paris-Sud, Orsay, France; M. Mitchell, J. Pattison and W.H.C. Ramsbottom of the British Geological Survey, Leeds; C. O'Riordan of the National Museum of Ireland, Dublin; R. B. Rickards of the Sedgwick Museum, Cambridge; P. Sartenaer of l'Institut Royal des Sciences Naturelles de Belgique, Bruxelles and C. D. Waterston of the Royal Scottish Museum, Edinburgh. Over several years members of the Photographic Unit of the British Museum (Natural History) have taken most of the photographs reproduced here, and A. Rissoné has provided technical assistance.

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Accepted for publication 2 September 1983

British Museum (Natural History)

An account of the Ordovician rocks of the Shelve Inlier in west Salop and part of north Powys

By the late W. F. Whittard, F.R.S. (Compiled by W. T. Dean)

Bulletin of the British Museum (*Natural History*), Geology series
Vol. 33 No. 1. Dec. 1979. 69pp. 38 figs. Large full-colour map

The late Professor W. F. Whittard, F.R.S., who died in 1966, devoted much of his life to the study of the Shelve Inlier, and his great monograph on its trilobites remains fundamental. The area, in west Salop (including a small part of north Powys), was the scene of famous early geological studies by Murchison, and Lapworth. By Palaeozoic standards it is in places richly fossiliferous, and exhibits the best continuous Ordovician succession in Britain, one which is indeed amost complete. This classic area is of continuing interest, not only to professionals but also to amateur geologists and students, few of whom complete their studies without at least one field visit; but amazingly this is the first detailed map ever to be published. That the work of Whittard, now made available through the efforts of Professor W. T. Dean of Cardiff, is authoritative there can be no doubt: for over thirty-five years he studied these rocks, unravelling their complexities and perfecting his map.

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By A. Williams

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The Llandovery Series of the Type Area

L. R. M. Cocks, N. H. Woodcock,
R. B. Rickards, J. T. Temple &
P. D. Lane

Geology series Vol 38 No 3 29 November 1984

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

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29 NOV 84

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Geol.)

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The Geology Series is edited in the Museum's Department of Palaeontology
Keeper of Palaeontology: Dr H. W. Ball
Editor of the Bulletin: Dr M. K. Howarth
Assistant Editor: Mr D. L. F. Sealy

ISBN 0 565 07002 9
ISSN 0007-1471

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Geology series
Vol 38 No 3 pp 131–182

Issued 29 November 1984

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The Llandovery Series of the Type Area

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Bull. Br. Mus. nat. Hist. (Geol.) **38** (3): 131–182

Issued 29 November 1984

Synopsis

The stratigraphy, fossils and correlation of the Llandovery area, Dyfed, Wales, are reviewed and its status assessed as the international type area for the lowest series of the Silurian System. A new lithostratigraphy is described, based on fresh mapping and exposures, of the Tridwr and Scrach Formations of Ashgill age, and of the Bronydd, Crychan and Trefawr Formations in the northern part of the Llandovery area, with the laterally equivalent Coldbrook and Goleugoed Formations in the central and southern parts of the area. Above these come the Rhydings, Wormwood and Cerig Formations, and the Wenlock age Gwernfelen Formation. The Derwyddon Formation is the lateral equivalent of the Rhydings and Wormwood Formations in the Pen-y-waun fault belt in the north-east.

The distributions of the major faunal elements are assessed and many new fossil records from the area noted, particularly of graptolites. A *Hirnantia* fauna is reported from the Scrach Formation. The stage divisions within the Llandovery Series are revised, with new faunas from the Rhuddanian Stage. The base of a new Aeronian Stage is defined within the Trefawr Formation at the base of the *triangulatus* Zone, and the base of the overlying Telychian Stage is redefined upwards and placed above the last record of *Eocoelia intermedia*, near the top of the Wormwood Formation, a horizon which approximately correlates with the base of the *turriculatus* Zone. The international correlation of the three stages is discussed.

Introduction

In 1977 the Silurian Subcommission of the International Union of Geological Sciences established in a postal vote that the term 'Llandovery' should be used for the lowest series of the Silurian System, following more than a century of usage. However, in 1979, during a field excursion to Britain, several members of the Subcommission were dissatisfied with the Llandovery area, Dyfed, Wales, as a type area, partly because some of the boundaries of the previously-defined stages (Cocks *et al.* 1970) were in isolated outcrops rather than in continuous sections, and partly because these stage boundaries had not been defined accurately enough in biostratigraphical terms. In addition the stratigraphy of the southern part of the Llandovery area had not been revised for over fifty years (Jones 1925). Accordingly, a small group was asked by the Subcommission to reinvestigate the whole Llandovery area, both north and south, and this is their report. The field work was done together in several periods from 1979 to 1983: N. H. Woodcock is primarily responsible for the lithostratigraphy and mapping, R. B. Rickards for work on the graptolites, J. T. Temple and L. R. M. Cocks for the earlier and later Llandovery brachiopods respectively, P. D. Lane for the trilobites and L. R. M. Cocks for coordinating the project.

This revision is opportune for several reasons, for example because the Forestry Commission has created several kilometres of continuous exposure in new forestry tracks in the area, which we have been able to evaluate, and also because research work over the past twenty years on rocks of Llandovery age, both in other parts of Britain and elsewhere, has led to a large new reservoir of knowledge on shelly, graptolitic and other faunas, many of which have been found in abundance in the present study. We have completely remapped the area, established a new lithostratigraphy (Fig. 1) and a new chronostratigraphy, and integrated these with the established international biostratigraphy. We conclude that the Llandovery area is fully suitable to continue as the international standard for the lowest series of the Silurian System.

History of Geological Studies in the Type Llandovery area

The Llandovery district has long been the standard British and international reference area for rocks of what are now termed Lower Silurian age. R. I. Murchison published his classic 'Silurian System' in 1839, in which there are five closely-printed pages (pp. 350–355), a general view (fig. 66) and two coloured geological sections (pl. 34, figs 1 and 3) describing the results of his three visits to the Llandovery district in 1833, 1834 and 1835. In Part II of the work, 'Organic Remains', Murchison himself and his colleagues J. de C. Sowerby,

<table>
<tr><th>JONES (1925)</th><th>JONES (1949)</th><th colspan="3">NEW TERMINOLOGY</th></tr>
<tr><th>SOUTHERN
"Wenlock"</th><th>NORTHERN
"Wenlock"</th><th>NORTHERN
Gwernfelen Fm</th><th>CENTRAL
Gwernfelen Fm</th><th>SOUTHERN
Gwernfelen Fm</th></tr>
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<tr><td>A3</td><td rowspan="2">Ab</td><td rowspan="2">Bronydd Fm</td></tr>
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<tr><td>A1</td><td>Aa</td><td>Scrach Fm</td><td>Scrach Fm</td><td>Scrach Fm</td></tr>
<tr><td>"Bala"</td><td>"Bala"</td><td>Tridwr Fm</td><td>Tridwr Fm</td><td>Tridwr Fm</td></tr>
</table>

Fig. 1 New lithostratigraphical terminology compared with those of Jones (1925) for the southern Llandovery area and Jones (1949) for the northern Llandovery area. The Tridwr and Scrach Formations are of Ashgill age and the Gwernfelen Formation is of Wenlock age.

Lonsdale and others described and illustrated twenty species of brachiopods, three gastropods, four nautiloids, a trilobite and two corals from the type Llandovery area (plus others from the overlying beds of Wenlock age at Llandovery). Although Murchison initially miscorrelated these 'Llandovery Building Stones' with the Caradoc of Shropshire, this error was corrected after the work of Sedgwick, Aveline, Ramsay and Salter, who between 1852 and 1854 (e.g. Salter & Aveline 1854) established the existence of an unconformity in

Shropshire between what is now known as the Silurian and the underlying rocks. These post-Caradoc, sub-Wenlock rocks were initially termed 'May Hill Rocks', but it was quickly realized that the rocks at May Hill, Gloucestershire, correlated only with the upper part of the sequence present at Llandovery, which was being mapped more precisely by W. T. Aveline for the Geological Survey in 1855–6. Thus the Geological Survey maps of 1857 were the first publications to use the term 'Llandovery' (divided into Upper Llandovery and Lower Llandovery) in a time-stratigraphical sense. Since Murchison was intimately associated with the Government surveyors (and himself joined the Geological Survey as Director-General in 1855), it was no surprise that he adopted the Survey terminology in a variety of papers, for example that on the Oslo region in Norway (1858), and in a revised edition of 'Siluria' (1859). Henceforth, the Llandovery became, and has remained, the standard for the lower part of what is now the restricted Silurian System both in Britain and elsewhere, and it is notable that Lapworth (1879: 14) in his original definition of the Ordovician System took it up to 'the base . . . of the Lower Llandovery.'

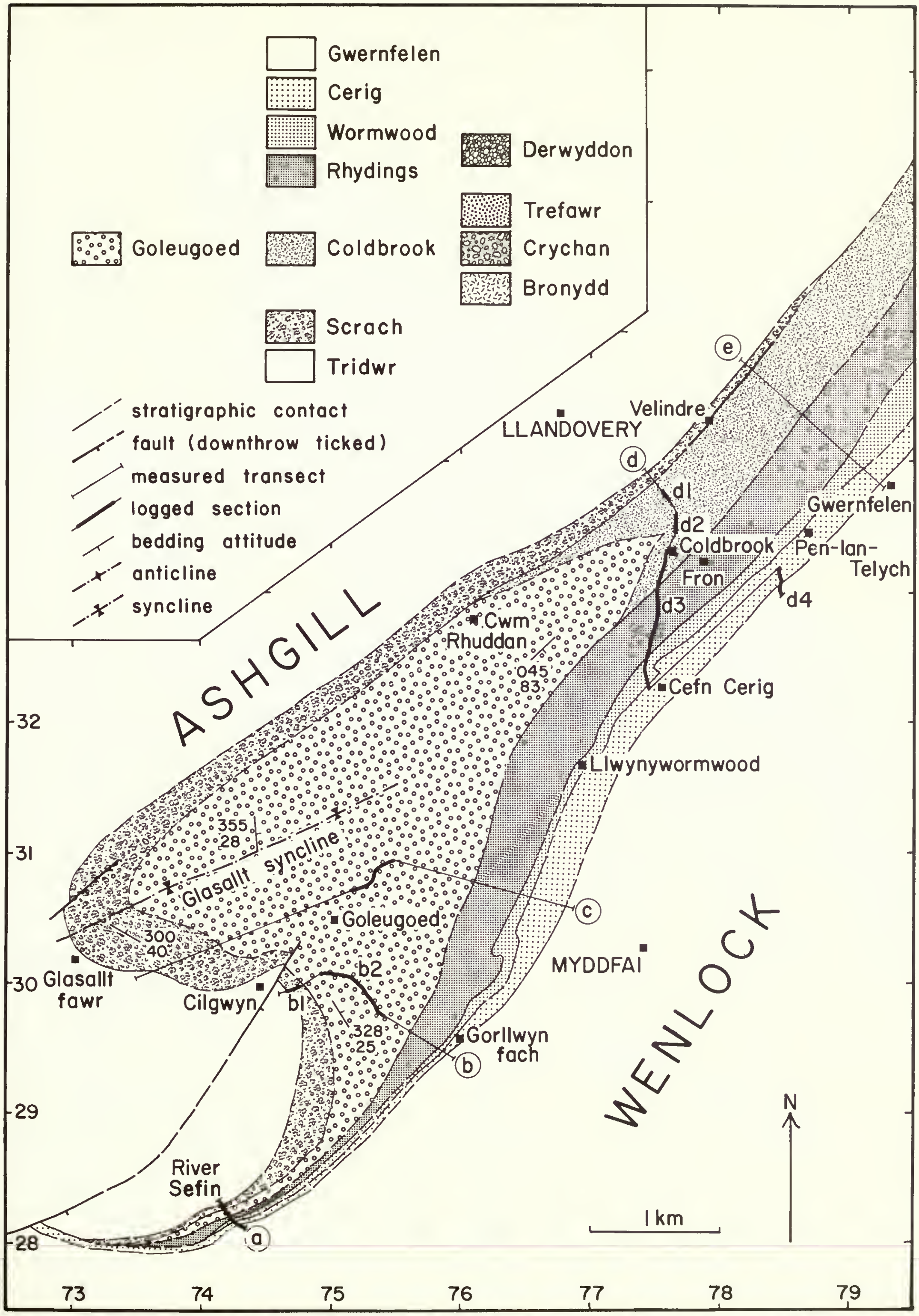
The first major revision of the Llandovery area after Aveline and Murchison was that by O. T. Jones, who mapped the area from 1915 onwards. He published this revision in two parts, the first paper on the southern half of the area (1925), and the second on the northern half (1949). In his first paper he divided the old Lower Llandovery into two parts, called Lower and Middle, separated by what he identified as an unconformity, and he established a series of divisions labelled A_1 to A_4 for the Lower Llandovery, B_1 to B_3 for the Middle Llandovery and C_1 to C_6 for the Upper Llandovery (Fig. 1). However, Jones had problems in extending these lithostratigraphical divisions over the area as a whole, and when he eventually published on the northern half of the Llandovery area (1949), he divided the Lower Llandovery there into Aa, Ab and Ac and the Upper Llandovery into Ca, Cb and Cc, with an undivided Middle Llandovery.

Although Jones (1928) had published on the plectambonitaceans from the area, the main part of his brachiopod collections was studied by A. Williams, who published what has become a classic paper (1951), with formal descriptions of 39 taxa and records of 86 different brachiopod species and subspecies, including the first account of the evolution of *Stricklandia*. Subsequent to Williams' work, the previously-defined lithostratigraphical units of Jones (C_1 etc.) have been employed as biostratigraphical subzones, and used as standard correlation units for the world as a whole (e.g. Berry & Boucot 1970 for North America). From a desire to attain more uniform terminology, such as that employed elsewhere in the Lower Palaeozoic, Cocks *et al.* (1970) divided Llandovery time into four stages, each with a base defined in the southern part of the Llandovery type area, apart from the basal stage, the Rhuddanian, which was taken from the base of the *persculptus* graptolite zone at Dob's Linn, Scotland. These stages were used as standard in the Geological Society's correlation chart of the Silurian rocks of the British Isles (Cocks *et al.* 1971).

A substantial number of publications in the last thirty years have described one or more fossil species each from the type Llandovery area; some of these papers are detailed below in the section on biostratigraphy, but until now there have been no other stratigraphical revisions of the area, apart from the unpublished sedimentological study by M. A. Woollands (1970) and short field guides (e.g. Cocks 1971). Woollands established that Jones had been mistaken in identifying an unconformity beneath his Middle Llandovery.

Lithostratigraphy

A formal lithostratigraphy is established here for the Llandovery Series rocks and some adjacent units, based on mapping and on measured lithological logs. The outcrop pattern of the new formations is shown in Figs 2 and 3 and their mutual relations in a south-west to north-east section in Figs 4 and 68 (p. 172). Many of the formation boundaries correspond closely to contacts mapped by Jones (1925, 1949) and Woollands (1970). However, we have subdivided the sequence less than they did, without formal recognition of those subtle lithological distinctions which cannot be mapped for more than a kilometre or so.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Goleugoed
Coldbrook
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stratigraphic contact
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measured transect
logged section
bedding attitude
anticline
syncline
ASHGILL
WENLOCK
LLANDOVERY
Velindre
Coldbrook
Fron
Gwernfelen
Pen-lan-Telych
Cwm Rhuddan
Cefn Cerig
Llwynywormwood
Glasallt syncline
Goleugoed
Glasallt fawr
Cilgwyn
MYDDFAI
Gorllwyn fach
River Sefin
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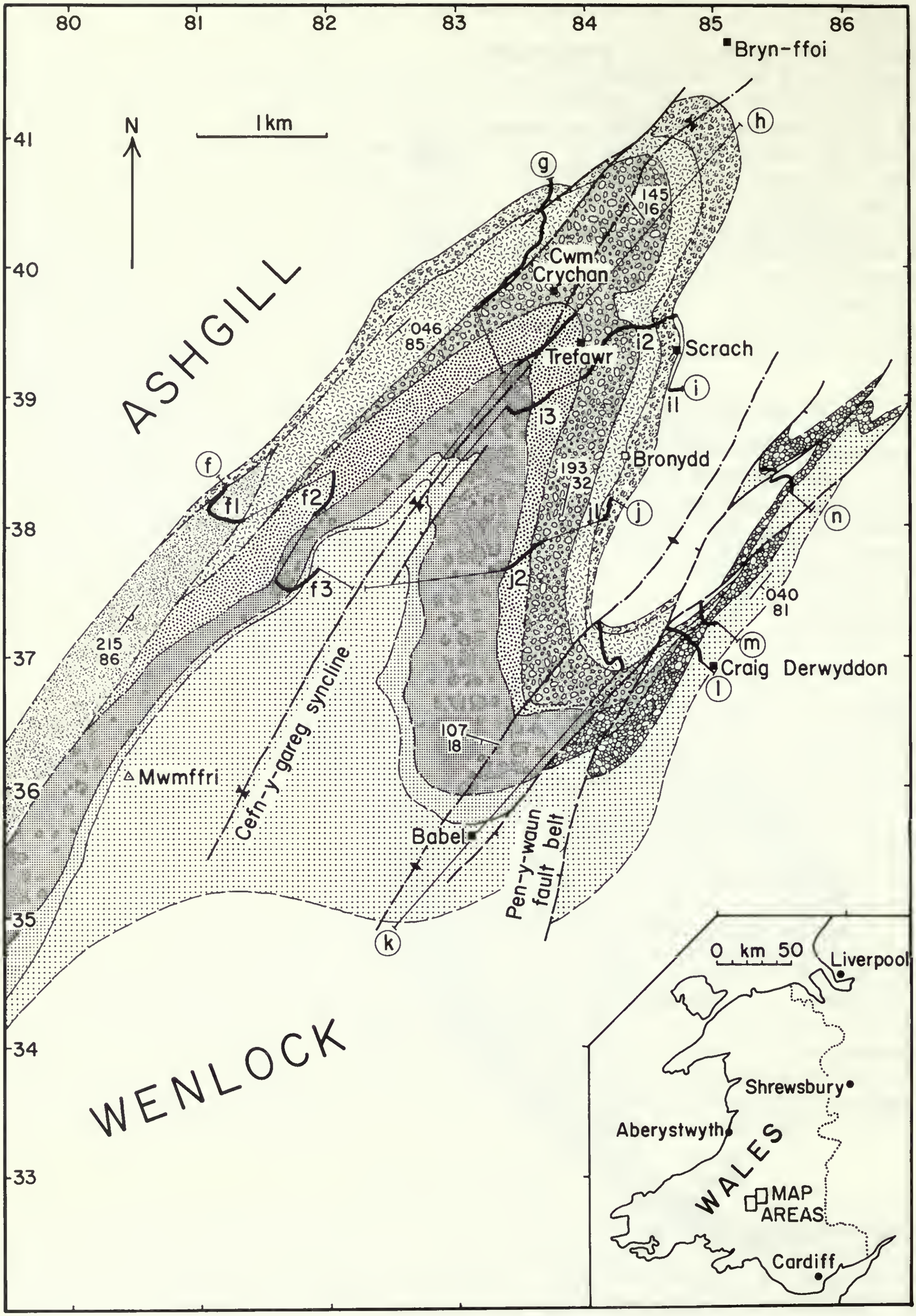
Fig. 2 Geological map of the southern part of the Llandovery area, showing transects a to e. The measured parts of the transects are shown as thicker lines; the thinner lines link the appropriate measured sections to the total transects shown on Fig. 4, pp. 138–9. The numbered 1 km squares of the National Grid are shown: they all fall within the SN 100 km square.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WENLOCK
Cwm Crychan
Trefawr
Scrach
Bronydd
Craig Derwyddon
Mwmffri
Babel
Cefn-y-gareg syncline
Pen-y-waun fault belt
f
f1
f2
f3
g
h
i
i1
i2
i3
j
j1
j2
k
l
m
n
145 16
046 85
193 32
040 81
215 86
107 18
0 km 50
Liverpool
Shrewsbury
Aberystwyth
WALES
MAP AREAS
Cardiff

Fig. 3 Geological map of the northern part of the Llandovery area showing transects f to n. The key to the ornament is on Fig. 2.

We confirm the view of Woollands (1970) that the only angular unconformity in the Llandovery Series is that below Jones' Upper Llandovery. Even at this level there is apparently a conformable sequence everywhere except in the Pen-y-Waun fault belt and the possible continuation of the fault belt in the extreme south-west of the area (Figs 2–4). In particular, the new biostratigraphic control suggests that a full sequence may be present below the later Llandovery rocks in the central steeply-dipping belt near Llandovery itself (transects d and f in Fig. 4). The lateral variability in Jones' Lower and Middle Llandovery is therefore due to true lateral facies changes (Woollands 1970) and not to overstep (Jones 1925, 1949).

The formations are described and interpreted below approximately in order from oldest to youngest, with reference to the lithological logs in Fig. 4. Lithological details shown in Fig. 5 are not repeated here. Interpretations of the facies are based on those of Woollands (1970), with major modification only in the case of the Scrach Formation.

The *Tridwr Formation* is typified by the mudstones of Ordovician age in the core of the Noethgrug Anticline, south-east of Bronydd (Fig. 3). Here the mudstones commonly have intercalated shelly sandstones (e.g. transect i). Elsewhere in the area (e.g. transects a, g) the Ordovician mudstones at this level rarely contain sandstones and these sequences are only tentatively assigned to the Tridwr Formation. Along the northwestern boundary of the area, the mudstones have a strong planar fabric, mainly a tectonic cleavage. The Tridwr Formation probably represents mud-dominated deposition on a marine shelf. Occasional strong traction currents, probably storm-generated, produced winnowed sands, particularly near the south-east margin of the area.

The *Scrach Formation* is dominated by shales with numerous thin ripple-cross-laminated sandstones. Occasionally (e.g. transect g) the sandstone layers comprise the bulk of the rock. In two areas (transects c, h) thick sandstone/conglomerate lenses occur within the typical Scrach facies; these latter are the 'basal Llandovery sandstones' (A_1, A_a) of Jones (1925, 1949). Our new data suggest that the Scrach Formation is latest Ordovician (Hirnantian) in age. The lenticular or flaser bedded lithology is characteristic of shallow sub-tidal or in part even intertidal conditions. The coarse sand bodies might represent tidal bars or channels. The undoubted shallowing compared with the Tridwr Formation is thought to reflect the late Ordovician glacio-eustatic lowering of sea level (cf. Brenchley & Newall 1980).

The *Bronydd Formation* mainly comprises mudstones completely lacking lamination or even bioturbation structures. There are sporadic thin micaceous shelly sandstones, weathering to 'rottenstones'. The base of the formation where seen (transects g, i, k, l, m) is always an abrupt conformable contact with the Scrach Formation, usually with a tough siltstone immediately above the contact. The sand content increases up the section both as discrete sandstones and as dispersed grains in the mudstones. The Bronydd Formation represents mud-dominated deposition on a marine shelf with occasional storm events generating discrete sand beds. The sharp base of the formation may mark the rapid sea level rise subsequent to the latest Ordovician glacial event (Brenchley & Newall 1980). The coarsening-up sequence suggests a prograding sedimentation system, probably pro-deltaic.

The *Crychan Formation* is dominated by massive, poorly sorted muddy sandstones, always bioturbated and commonly containing dispersed pebbles. Occasional well-sorted sandstone beds occur, thinner than in the Bronydd Formation. The boundary with the Bronydd is gradational over 10 m or so (e.g. transect i). The Crychan Formation thins and fines down the north-west limb of the Cefn-y-gareg syncline. The Formation probably represents deposition on a more proximal part of a pro-delta lobe than the Bronydd Formation, but still in fully marine conditions. The sediment source was from the south-east. Traction currents were strong enough at times to roll pebbles across a cohesive mud substrate, and occasional storm events left thin winnowed sand beds.

The *Trefawr Formation* is rather varied, but is typically finer grained than the underlying Crychan Formation (e.g. transects i2 and i3). The dominant lithology is unlaminated sandy

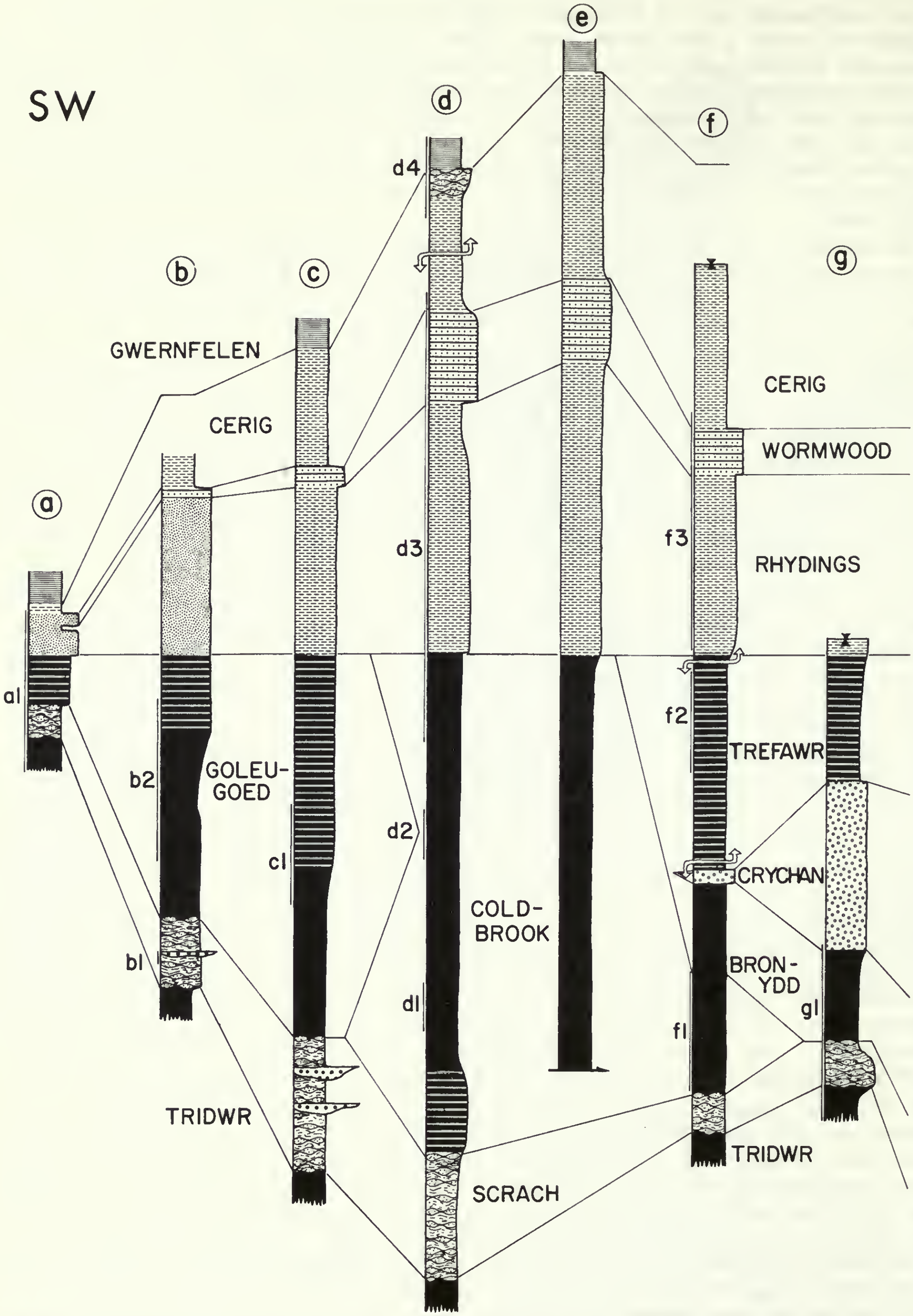
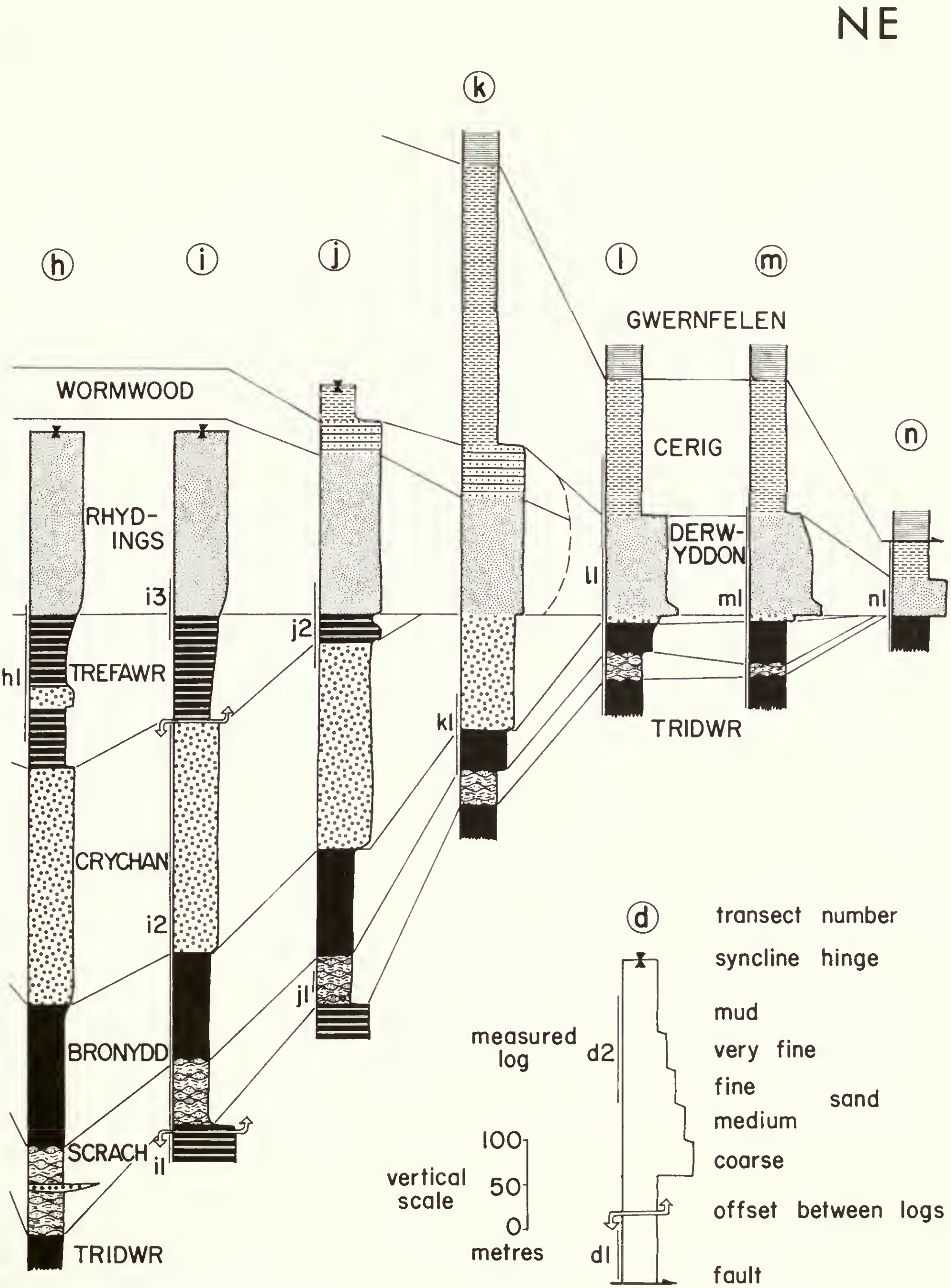

SW
ⓐ
ⓑ
ⓒ
ⓓ
ⓔ
ⓕ
ⓖ
GWERNFELEN
CERIG
WORMWOOD
RHYDINGS
GOLEU-
GOED
TREFAWR
CRYCHAN
COLD-
BROOK
BRON-
YDD
TRIDWR
SCRACH
a1
b1
b2
c1
d1
d2
d3
d4
f1
f2
f3
g1

Fig. 4 Transects a to n south-west to north-east across the type Llandovery area. The key to the ornament is shown on Fig. 5, p. 141. The vertical lines on the left of the various transects show the position of the continuously exposed and measured parts of the transects. The locations of


NE
k
h
i
j
l
m
n
GWERNFELEN
WORMWOOD
CERIG
RHYD-
INGS
DERW-
YDDON
i3
j2
ll
ml
nl
hl
TREFAWR
kl
TRIDWR
CRYCHAN
i2
jl
BRONYDD
SCRACH
il
TRIDWR
d
transect number
syncline hinge
mud
very fine
fine
medium
coarse
sand
measured
log
d2
100
50
0
vertical
scale
metres
dl
offset between logs
fault

the transects are shown on Figs 2 and 3 and the grid references of the ends of the measured sections are given in Appendix 3, p. 178.

mudstone similar to the Bronydd Formation but including more frequent micaceous calcareous sandstone beds. The formation generally coarsens up the section. Sandy mudstones with dispersed pebbles occur in the central part of the sequence in transect h (Figs 61, 62) and dominate the Trefawr Formation in the south-east (transect k). The Trefawr Formation, like the Crychan, fines on the north-west limb of the Cefn-y-gareg syncline (Fig. 3). Interpreted as a pro-delta marine sequence, the Trefawr represents more distal conditions than the underlying Crychan Formation, probably because of a lateral switch in the sediment supply. Probable storm sands were again produced.

The *Coldbrook Formation* is the lateral equivalent of the Bronydd, Crychan and Trefawr Formations in the central part of the Llandovery area, south-westwards of where the Crychan Formation thins to zero and fails to differentiate the finer Bronydd and Trefawr Formations. The Coldbrook comprises silty mudstones, often fissile owing to an imposed slaty cleavage. In transect e the stratigraphically highest parts of the Coldbrook are unlaminated, whereas lower parts are laminated with thin, parallel-laminated sandstones. Occasional thicker calcareous sandstone beds occur, and are locally abundant in the basal 100 m near transect d. These vertical variations cannot be mapped far along the strike. The Coldbrook Formation presumably represents marine clastic deposition further from the sediment supply than areas to the north-east and south-west. However, the total sediment thickness was not reduced (Fig. 4). High energy conditions occurred locally during deposition of the lowest part of the Formation.

The *Goleugoed Formation* is the lateral equivalent of the Coldbrook Formation in the south-west part of the Llandovery area. It is again dominated by mudstones, but includes a much higher proportion of thin sandstone beds and of dispersed sand than the Coldbrook. The average grain size and frequency of sand beds tends to increase up the section and these form locally mappable boundaries in transects b and c. Above the well-exposed parts of these transects occur muddy sandstone intervals but poor exposure prevents their lateral correlation. The Goleugoed Formation represents shallow marine deposition closer to a sediment source than the Coldbrook Formation. A pro-deltaic environment is suggested by sequences coarsening upwards, similar to those in the Bronydd/Crychan and Trefawr Formations, though no direct lithological correlation with the north-west area can be made.

The *Rhydings Formation* is mappable from north-east to south-west of the Llandovery area as relatively resistant sandy mudstones or muddy sandstones. These sediments are moderately to well sorted and often parallel-laminated, in contrast to the sandy facies in, for example, the Crychan or Goleugoed Formations. The lower boundary of the Rhydings is conformable over much of its outcrop length and is often gradational (e.g. transects h, i and j). As an angular unconformity develops at this level towards the Pen-y-waun fault belt (Fig. 4), the Rhydings Formation becomes thinner and coarser, and passes laterally into the Derwyddon Formation described below. A similar transition is seen above the unconformity in the Sefin River section at the south-west end of the area. The Rhydings Formation records open marine shelf deposition resulting from the well-documented late Llandovery marine transgression (Ziegler, Cocks & McKerrow 1968). The transgressed sea-floor topography still influenced sedimentation (Woollands 1970) with coarser, presumably shallower facies deposited on the existing pro-delta lobes (e.g. transects h, i and j) and finer-grained facies in the interlobe area above the Coldbrook Formation (e.g. transects d, f).

The *Wormwood Formation* consists of muddy sandstones and calcareous mudstones, more thinly and better bedded than the Rhydings (Figs 65, 66), but with beds more intensely bioturbated. The Formation is best distinguished in the southern Llandovery area (e.g. transect d). It is recognizable further north-east (e.g. transect f), though it may not be continuous there. As with the underlying Rhydings Formation, it is replaced laterally by coarser facies in the Pen-y-waun fault belt and in the extreme south-west of the area. The Wormwood Formation may represent open marine shelf conditions slightly shallower than

FACIES SYMBOL	FORMATION	LITHOLOGY	RANGE OF GRAIN SIZE	SORTING	COLOUR	BEDDING THICKNESS	SEDIMENTARY STRUCTURES
▒	Gwernfelen	muddy siltstones or very fine sandstone	clay to vf sand	moderate	grey/black	max 1cm	very fine (1 to 5mm) parallel lamination
▤	Cerig Rhydings	silty or sandy mudstones	clay to vf sand	moderate	greenish grey	max 4cm	parallel lamination, some bioturbation, some granule layers
▦	Wormwood	muddy sandstones	clay to m sand	poor	dark green to dark grey	max 40cm	well bedded, but poorly laminated, strong bioturbation, shell layers
░	Rhydings Derwyddon	sandstones or muddy sandstones	silt to vc sand	moderate /good	bluish or greenish grey	max 1m	parallel & cross lamination, ripples strong bioturbation, pebble layers
⁙	Crychan Trefawr Goleugoed	pebbly muddy sandstones with some calcareous sandst's	clay to pebbles	poor	bluish or greenish grey	0·5-2m	bioturbated, dispersed pebbles
			f to m sand	good	bluish grey	max 3cm	parallel lamination
≡	Crychan Trefawr Bronydd Goleugoed Tridwr	sandy mudstones with some micaceous sandstones	clay to f sand	moderate	dark grey	ave 1m	bioturbated, occasionally parallel laminated.
			f to m sand	good	bluish grey	max 30cm	poorly laminated occasionally graded
■	Coldbrook Bronydd Tridwr	silty mudstones with rare micaceous sandstones	clay or silt	moderate	dark grey	ave 1m	uniformly non-laminated (slaty in Coldbrook)
			f to m sand	moderate	light grey	max 5cm	poorly laminated occasionally graded
≋	Cerig Scrach	silty shales with thin sandstones	clay or silt	moderate	dark grey	ave 1cm	fissile
			vf to f sand	good	greenish grey	ave 1cm	ripple cross-lamination, surface trails.
◡	Scrach	sandstones / conglomerates	f sand to pebbles	good	greenish grey	ave 0·5cm	lenticular fining-up sequences, cross & parallel lamination

Fig. 5 Details of the sedimentary facies of the Llandovery Series and adjacent formations in the Llandovery type area. The facies ornaments to the left are those used in Fig. 4.

the Rhydings Formation, correlating with a more widely recognized marine regression at this time (Ziegler 1965, Woollands 1970).

The *Derwyddon Formation* is restricted to the Pen-y-waun fault belt in the east of the area (Figs 3, 4) and is the lateral equivalent of the Rhydings and Wormwood Formations further west and south. The formation is dominated by well-bedded sandstones, coarser and better sorted than in the Rhydings and Wormwood Formations. Parallel lamination is common and large-scale cross-stratification is present. Beds conspicuously rich in *Pentamerus* valves are common. The Derwyddon rests with angular unconformity on the eroded edges of the Crychan, Bronydd, Scrach and Tridwr Formations and is particularly coarse immediately above this contact. The formation records higher energy conditions than elsewhere in the Llandovery area at this time. This probably reflects shallower marine conditions along the recently submerged Pen-y-waun zone. This positive zone may have extended south-westward and joined the extreme south-west of the Llandovery outcrop (transect a). Here also a coarse lateral equivalent (unnamed) of the Rhydings/Wormwood Formations overlies a marked unconformity.

The *Cerig Formation* comprises silty mudstones similar to some lithologies in the Rhydings Formation but less well-cemented and resistant. The mudstones are commonly parallel-laminated and occasionally bioturbated, with sporadic large-scale slumped zones. The upper part of the Formation in the central area (e.g. transect d) has numerous thin intercalations of fine cross-laminated sandstones. The Cerig Formation blankets the whole of the underlying Llandovery sequence, even in the shallow south-eastern areas. It probably records a further transgressive pulse, resulting in open marine shelf deposition over the whole area. The cross-laminated sandstone facies in the central area suggest shallowing there late in Llandovery time.

The *Gwernfelen Formation* comprises uniformly finely laminated muddy siltstones of Wenlock age (e.g. transect d). Over most of the area these rocks overlie the Cerig Formation conformably. In the Pen-y-waun fault belt contacts of Wenlock rocks with lower horizons are probably faulted, as is the Wenlock/Ordovician contact to the north-east. The origin of the Gwernfelen facies is problematical. It is common elsewhere in the British Wenlock and similar sediments have been interpreted as distal turbidites in a deep basin (Piper 1972). This seems an unlikely interpretation in this area. Constant weak traction currents ('contour currents') flowing across a deepened marine shelf are another possibility.

Structure

The Llandovery Series rocks have been affected by only one important episode of deformation, probably culminating in latest Silurian to mid-Devonian time. The resulting structure is relatively simple and is directly visible on the geological map (Figs 2 and 3).

At the north-eastern end of the area a major syncline/anticline pair plunges gently south-west. The folds have a wavelength of about 3·5 km. They are asymmetric to the south-east, with steep limbs younging south-east flanking a gently dipping limb younging north-west. A weak axial-planar cleavage dips steeply north-west, but is often absent in the gentle limb. The steep limbs are cut by sub-vertical faults striking north-east to south-west, mostly downthrowing to the south-east. The south-eastern steep limb, named the Pen-y-waun fault belt, coincides with an unconformity below the later Llandovery rocks (Figs 4 and 68).

Another syncline-anticline pair is seen at the south-western end of the area. This pair has wavelength of about 3 km, is again asymmetric to the south-east, but here plunges gently north-east. A steep fault striking north-east to south-west cuts the anticline hinge and downthrows to the south-east. The south-eastern steep limb is again a zone of sub-Upper Llandovery unconformity (Figs 3, 4), suggesting that it may connect structurally, through steep intervening Wenlock and Ludlow rocks, with the Pen-y-waun fault belt further north-east.

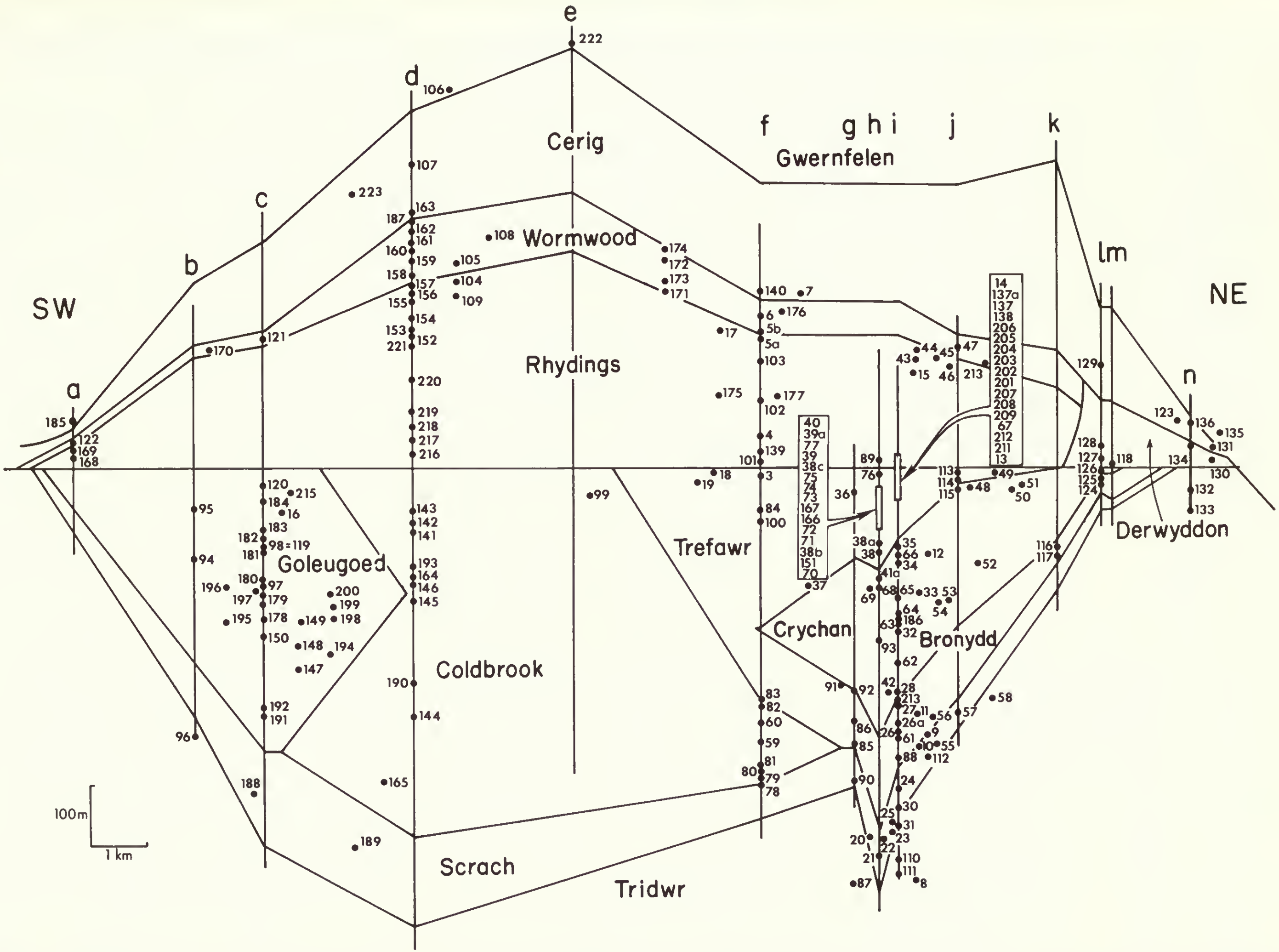

SW
NE
a
b
c
d
e
f
g h i
j
k
lm
n
Cerig
Gwernfelen
Wormwood
Rhydings
Trefawr
Goleugoed
Coldbrook
Crychan
Bronydd
Derwyddon
Scrach
Tridwr
100m
1 km

Fig. 6 Fossil locality numbers projected onto a SW–NE section through the Llandovery area. Transects a to n are located on Figs 2 and 3, and gaps and offsets in the transects are shown on Fig. 4, for example the various subsections of transect i. Grid references of the localities are given in Appendix 2, p. 177, and of the ends of the measured parts of the transects in Appendix 3, p. 178.

The central part of the Llandovery area shows no major folding, just a steeply-dipping sequence younging continuously to the south-east.

About half the stratigraphic logs come from gently dipping sequences where the weakness or absence of cleavage suggests only minor tectonic modification of the original compacted thickness. The measured thicknesses in logs taken in steeply-dipping sequences should be more cautiously interpreted. However, even here, much of the folding was accomplished by slip on bedding planes (rather than internal strain of layers) and stratigraphic thicknesses are probably essentially unchanged.

Biostratigraphy

The chief fossil groups from the Llandovery type area are treated individually below, but the faunas from the beds immediately below and above the rocks of Llandovery age in the area need brief discussion here.

It has been known from the time of Jones (1925) that mid-Ashgill faunas are to be found in what we term the Tridwr Formation. These include such forms as *Sampo ruralis* (Reed), *Christiania tenuicincta* (M'Coy), *Chonetoidea papillosa* Jones and *Orthograptus truncatus* (Lapworth), and many more which together indicate a Rawtheyan age for the formation. However, previously unreported are faunas which we have found in the succeeding Scrach Formation (e.g. from Locality 90); this is the formation which includes the restricted and lensing A_1 Sandstone of Jones in the southern part of the area. These faunas include *Eostropheodonta hirnantensis* (M'Coy), *Hirnantia sagittifera* (M'Coy), *Plectothyrella crassicostis* (Dalman), *Dalmanella testudinaria* (Dalman) and an undetermined bryozoan, and can be identified as typical *Hirnantia* faunas of latest Ordovician, Hirnantian age. This is of immense stratigraphical importance, lying as it does under the Bronydd Formation which has a *persculptus* or *acuminatus* Zone graptolite fauna near its base. Other localities in the Scrach Formation have yielded fragments of cyclopygid trilobites, which strengthen the case for a pre-Silurian age.

Above the type Llandovery rocks, the lower Wenlock mudstones and siltstones, termed here the Gwernfelen Formation, have yielded a variety of forms, in particular the graptolite *Monoclimacis vomerina basilica* (Lapworth) from Loc. 185, indicating a basal Wenlock *centrifugus* Zone age. The formation also includes local shelly faunas including forms such as *Leangella, Skenidioides, Clorinda, Encrinurus* and others.

(a) Graptolites

Figs 7 and 19 illustrate the considerable extent to which the Llandovery strata have a graptolite biostratigraphical framework, far greater, in fact, than had hitherto been supposed. The earliest graptolites we have obtained show that the age of the Tridwr Formation is uppermost Ordovician, with an association of *Orthograptus amplexicaulis* (Hall), *Climacograptus angustus* (Perner), ?*C. supernus* Elles & Wood, *Dendrograptus* sp., *Chaunograptus* sp. and ?*Mastigograptus* sp. A horizon very low in the Bronydd Formation (Loc. 88) has yielded a single well-preserved specimen of *Climacograptus normalis* Lapworth, the dimensions and shape of the proximal end and complete median septum of which suggest a horizon certainly no higher than the *acuminatus* Zone, and probably as low as the *persculptus* Zone.

Dating of the bulk of the Bronydd Formation is not easy on direct evidence, although graptolites have been obtained from several localities. But the fact that it is overlain to the north-east by the Crychan Formation, which is largely referable to the *cyphus* Zone (see below), seems to indicate that the Bronydd fauna of *C.* cf. *normalis, Climacograptus rectangularis* M'Coy, *C. angustus, Rhaphidograptus toernquisti* (Elles & Wood) and *Glyptograptus* sp. corresponds approximately to the *atavus* and *acinaces* Zones. There are no direct indicators of the *cyphus* Zone as there are in the overlying beds. Correlation of the lower part of transect f with the lower part of transects g, h and i is feasible, despite the lithological change south-westwards to the Coldbrook Formation, because Loc. 81 yields

TRANSECTS & LOCALITY NUMBERS														graptolites, rhabdopleurans and chitinous hydroids
a	b	c	d	e	f	g	h	i	j	k	l	m	n	
								13						Orthogroptus omplexicaulis (Holl)
													133	Climocogroptus supernus E. & W.
													133	Mostigograptus sp.
							70	31						Dendrograptus sp. / Dictyonemo sp.
					81			31						Climocogroptus angustus E. & W.
					37			88,26						Climocogroptus narmolis Lopw.
					59			14						Glyptogroptus sp.
			141, 164 142		81									P.(Metoclimacograptus) fidus/pictus K & M.
					5,81,101	S	N	N						Rhophidogroptus taernquisti E. & W.
					18			26,35						Climocograptus rectonguloris M'Coy
						37								Pribylograptus incommodus Törnq.
								35						P.(Metaclimocagroptus) hughesi (Nich.)
								35						Atavogroptus strochoni Hutt & Rick.
			157					14,35					131	Monogroptus sp.
			145, 141				70	31						Climacogroptus sp.
							70							Logorogroptus ocinoces (Törnq.)
							70							Monogr. ousterus vulgoris Hutt
							70							Dictyonemo corrugotellum Lopw.
							151							Diplograptus elongotus Churkin & C.
							151							Pseudoglyptograptus sp. I. Rick. 1972
					100									Monogroptus revolutus Kurck
					100									Monogr. triangulotus seporatus Sud.
			142		100									Manogr. triangulotus fimbriotus Nich.
			146											Climocogroptus olternis Pockhom
			145		101		S							P.(Clinoclimocogroptus) retroversus B.&R.
			141, 146				72							Manogr. austerus sequens Hutt
							166,S							G.(Pseudoglyptograptus) vas B. & R.
							166							G. tomariscus lineoris (Perner)
							73							Rastrites peregrinus Borr.
							166							Orthogr. insectiformis Nich.
			143											Glyptogr. incertus E. & W.
			142, 146		100		73							Diplogr. magnus H. Lapw.
			143											Petalogr. minor Elles
			142											G. t. tamariscus Nich.
			143											Orthogr. cyperoides Törnq.
	94				84	38	75							indeterminote biseriols
							75							Dictyonema venustus Lopw.
							38c							Discograptus sp.
							38c							Atavograptus otovus (Jones)
								67						Karemogroptus sp.
							39a							Pristiograptus reguloris (Törnq.)
						36								Orthogroptus sp.
					101									Monogr. convolutus (Hisinger)
								14						Orthogr. bellulus
								14						Rastrites linnoei
							89			& Sefin River				Monogroptus sedgwickii (Portl.)
														Logaragroptus tenuis (Portl.)
													131	Monogr. runcinotus Lopw.
													131	Rhobdopleuro sp. nov.
													133	chitinous hydroids
					140	36								P. (Metoclimocogroptus) sp.

Fig. 7 Graptolite records tied to locality numbers and the transects shown in Figs 2–4. The symbol N indicates numerous localities on this transect and S indicates several localities.

Pseudoclimacograptus (*Metaclimacograptus*) cf. *fidus* Koren' & Mikhailova or, possibly, *P.* (*M.*) *pictus* Koren' & Mikhailova, both of which occur in the *acuminatus* Zone of the U.S.S.R. Thus a horizon quite low in the Coldbrook Formation is probably referable to the *acuminatus* Zone. The Bronydd Formtion probably ranges in age from the *persculptus* or *acuminatus* Zone near its base to the *acinaces* or low *cyphus* Zone at its top.

The Crychan Formation has yielded *Pseudoclimacograptus* (*Metaclimacograptus*) cf. *hughesi* (Nicholson) and *Glyptograptus* ex gr. *tamariscus* (Nicholson) in the middle, and *P.* (*M.*) *hughesi, Climacograptus* sp., *C.* ?*rectangularis*, cf. *R. toernquisti, Atavograptus* ?*strachani* (Hutt & Rickards) and *Monograptus* sp. towards the top, suggesting that the bulk of the formation is referable to the *cyphus* Zone although the lower part could be in part *acinaces* Zone. A locality at the very top of the Crychan Formation (Loc. 35, transect i) has yielded *A.* ?*strachani* and possibly triangulate monograptid thecae. The latter thecal type first appears in the upper part of the *cyphus* Zone and becomes more typical of higher levels.

Graptolites are most common in the Trefawr Formation and equivalents, occurring in abundance at numerous localities, and they allow recognition of the *cyphus, triangulatus, magnus* and *convolutus* Zones with good lower boundaries for the first two of these zones. The base of the *triangulatus* Zone can be taken at the base of Loc. 72 (transect h) within the Trefawr Formation. Above this level occurs *Monograptus austerus sequens* Hutt (Loc. 72), a *triangulatus* Zone form; below this level *Monograptus* cf. *austerus vulgaris* Hutt, *Diplograptus elongatus* Churkin & Carter, ?*Pseudoglyptograptus* sp. 1 (*sensu* Rickards 1972) and cf. *Lagarograptus acinaces* Törnquist (or ?*C. cyphus*) indicate the *cyphus* Zone.

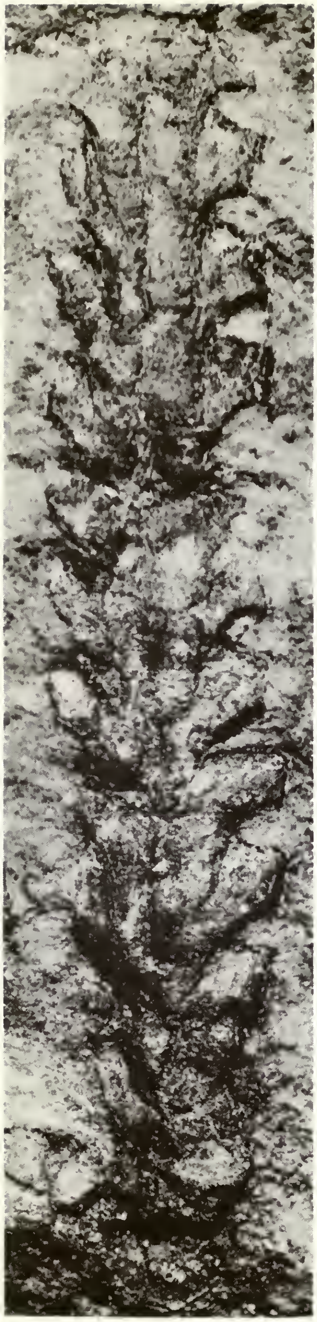
Loc. 100, on transect f, is at the same stratigraphical level as Loc. 72, and yields *Monograptus* cf. *revolutus* Kurck *s.s., Monograptus triangulatus* ?*separatus* Sudbury, *M. t.* ?*fimbriatus* (Nicholson), *R. toernquisti* and *Diplograptus* cf. *magnus* Lapworth, which also indicate a *triangulatus* Zone attribution.

The best sequence through the *triangulatus* Zone into the *magnus* Zone is in transect h, where the base of the *magnus* Zone is marked by the incoming of *Glyptograptus* (*Pseudoglyptograptus*) *vas* Bulman & Rickards (Fig. 13), *Orthograptus insectiformis* (Nicholson) and *Glyptograptus tamariscus* cf. *linearis* (Perner) at the base of Loc. 166. Various *D. magnus*-like forms occur immediately above this and continue to be associated with *G.* (*P.*) *vas*.

The *magnus* Zone fauna is well represented at numerous other localities and is typified by the eponymous taxon and by *Glyptograptus* (*Pseudoglyptograptus*) *vas* Bulman & Rickards and *Orthograptus insectiformis* Nicholson. Numbers of other species occur which are in accord with the attribution of strata above the base of Loc. 166 (transect h) to the *magnus* Zone (Figs 7, 19). A good *magnus* Zone assemblage also occurs on the Cefn Cerig Road section (transect d), where it is also underlain by strata possibly referable to the *triangulatus* Zone which contain *Climacograptus* ?*alternis* Packham.

Most of the Trefawr Formation on the transect h section above Loc. 166 yields a *magnus* Zone fauna, but Loc. 36, stratigraphically just below the *sedgwickii* Zone of the Rhydings Formation, yields a *convolutus* Zone fauna: Jones (1949) recorded *Monograptus decipiens* Törnquist, *M.* cf. *lobiferus* M'Coy, *Pristiograptus regularis* (Törnquist) and *Orthograptus cyperoides* Törnquist, while we have found *Orthograptus* sp., *R. toernquisti* and ?*Pseudoclimacograptus* sp. On the main Trefawr track nearby (transect h) the change to *convolutus* probably takes place at about Loc. 39, the highest probable *magnus* level being at Loc. 74. Between Locs 74 and 39 there are at least 30m of strata, so far yielding only undiagnostic, yet not infrequent, graptolites.

The *sedgwickii* Zone is indicated at two localities, both near the base of the Rhydings Formation. Loc. 89 (transect h) yields *M.* cf. *sedgwickii* Portlock, and the collection from Loc. 14 (transect i) contains *Orthograptus* cf. *bellulus* Törnquist, *Rastrites* aff. *linnaei* Barrande, *Glyptograptus* sp. and *Monograptus* sp. *s.s.* Loc. 101 (transect f) yields *M.* aff. *convolutus* (Hisinger), so that it is probable that the base of the *sedgwickii* Zone is only a few metres above the base of the Rhydings Formation. The Sefin River also yields *M. sedgwickii* and *Lagarograptus tenuis* (Portlock) at the same level.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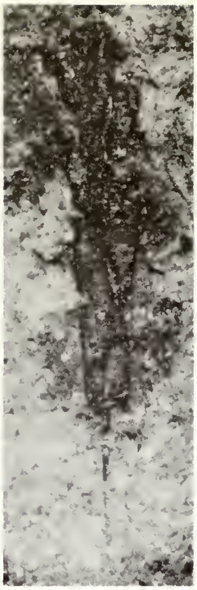
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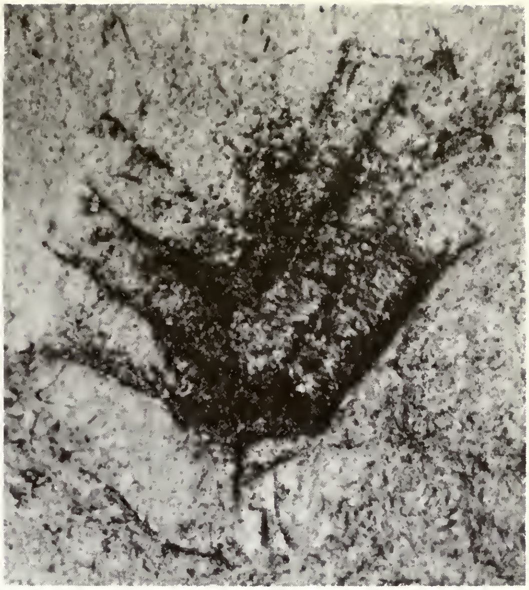
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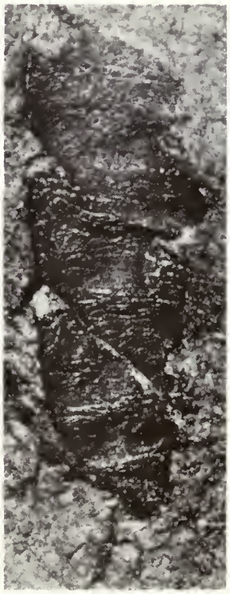
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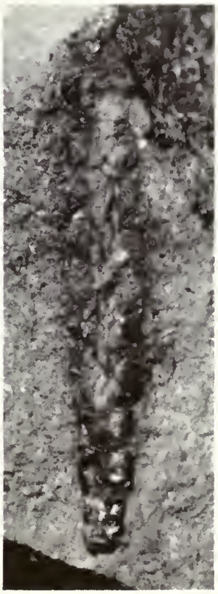
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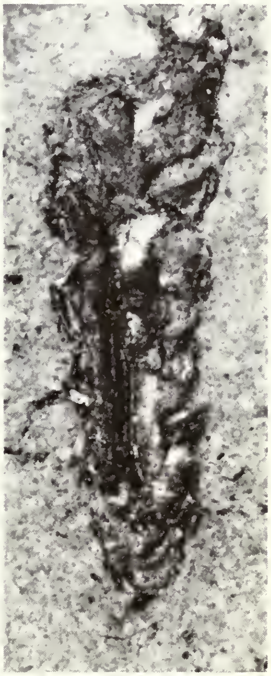
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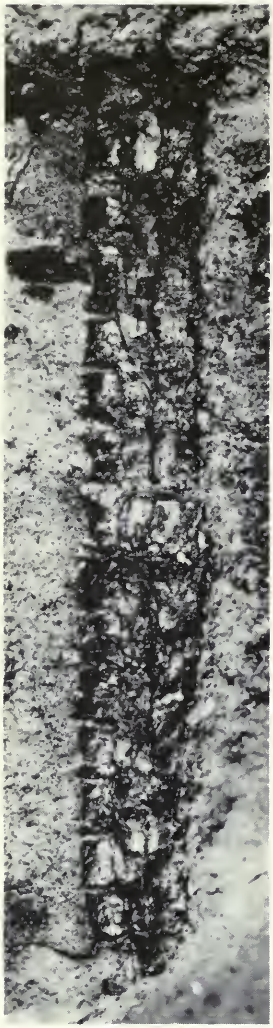
Figs 8–13 Graptolites from the type Llandovery area (SM = Sedgwick Museum, Cambridge). Fig. 8, *Diplograptus* cf. *magnus* H. Lapworth, 1900, proximal region in partial relief, somewhat distorted; SM A109544, ×20; *triangulatus* Zone, Trefawr Formation, Loc. 100. Fig. 9, *Rhaphidograptus toernquisti* (Elles & Wood, 1906), obverse view of proximal end in low relief, showing sicula and virgella; SM A105946, ×15; *cyphus* Zone, Trefawr Formation, Loc. 38. Fig. 10, *Petalograptus minor* Elles, 1897, proximal end with virgella; SM X330, ×20; *magnus* Zone, Coldbrook Formation, Loc. 143. Fig. 11, *Climacograptus ?alternis* Packham, 1962, reverse view of proximal end in three dimensions; SM X329, ×20; *triangulatus* Zone, Coldbrook Formation, Loc. 146. Figs 12, 13, *Glyptograptus* (*Pseudoglyptograptus*) *vas* Bulman & Rickards, 1968; Fig. 12, proximal end in low relief; SM X331, ×10; *magnus* Zone, Trefawr Formation, Loc. 166; Fig. 13, proximal region in low relief; SM A105938, ×20; *magnus* Zone, Coldbrook Formation, Loc. 142.



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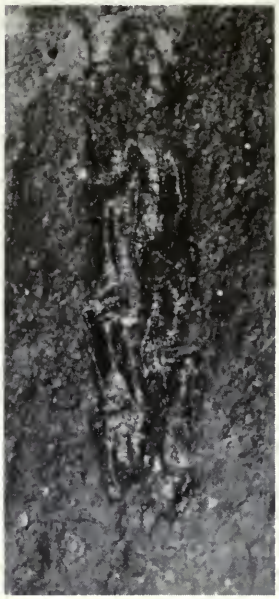

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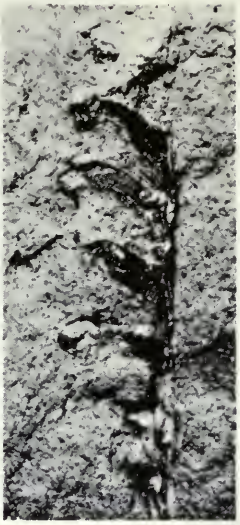

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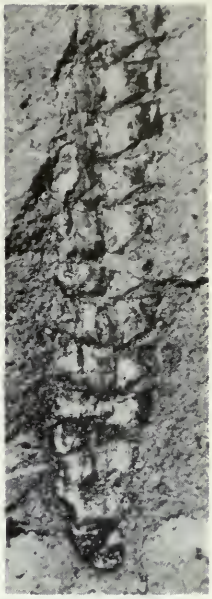

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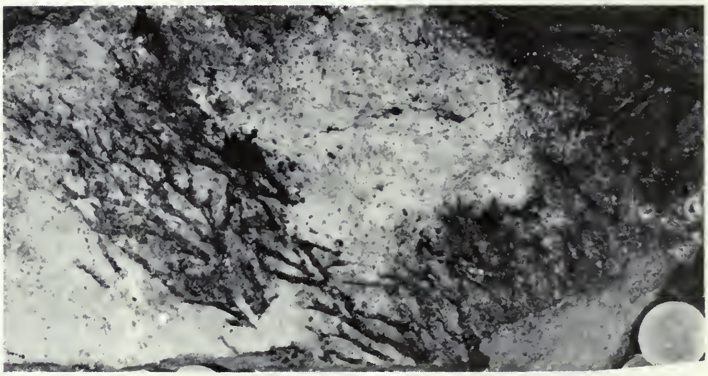

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Figs 14–18 Graptolites from the type Llandovery area, cont. Fig. 14, *Rhaphidograptus toernquisti* (Elles & Wood, 1906), distal thecae in low relief; SM X332, ×10; *cyphus* Zone, Trefawr Formation, Loc. 38. Fig. 15, *Pseudoclimacograptus* (*Clinoclimacograptus*) *retroversus* Bulman & Rickards, 1968, proximal end in moderate relief; SM A105951, ×20; *triangulatus* Zone, Coldbrook Formation, Loc. 81. Fig. 16, *Monograptus triangulatus* cf. *fimbriatus* (Nicholson, 1868), early mesial thecae in low relief; SM A105723, ×10; *magnus* Zone, Coldbrook Formation, Loc. 142. Fig. 17, *Glyptograptus* (*Pseudoglyptograptus*) ?sp. 1 *sensu* Rickards (1972), proximal and mesial regions in low relief; SM X334, ×10; *cyphus* Zone, Trefawr Formation, Loc. 151. Fig. 18, *Koremagraptus* sp., fragmentary part of large rhabdosome; SM A105954, ×3; *magnus* Zone, Trefawr Formation, Loc. 67.

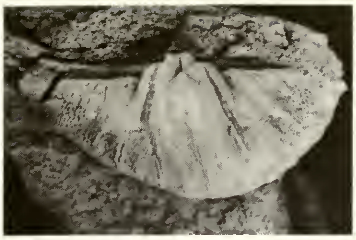
Above the Rhydings Formation, graptolites have proved to be rare. But *Monograptus runcinatus* Tullberg occurs near the base of the Cerig Formation (Loc. 131, transect n) and ?*Pseudoclimacograptus* (*Metaclimacograptus*) sp. at Loc. 140, transect f; thus we would place the base of the Cerig Formation near the base of the *turriculatus* Zone.

Graptolite Zones graptolites rhabdopleurans & chitinous hydroids	supernus	"persculptus"	acuminatus	"atavus"	"acinaces"	cyphus	triangulatus	magnus	"argenteus"	convolutus	sedgwickii	turriculatus
Orthograptus amplexicaulis (Hall)	●											
Climacagraptus supernus E. & W.	?											
Mastigagraptus sp.	?											
Dendrograptus sp. / Dictyonema sp.	●					●						
Climacagraptus angustus E. & W.	●		●									
Climacograptus normalis Lapw.		●		cf.		aff.						
Glyptagraptus sp.				●							●	
P.(Metaclimacagraptus) fidus/pictus K & M.			●									
Rhaphidagraptus toernquisti E. & W.			cf.	●	●	●	●	●	●	●	●	
Climacagraptus rectangularis M'Coy				●	?			?		cf.		
Pribylagraptus incommodus Törnq.						●						
P.(Metaclimacograptus) hughesi (Nich.)					cf.	cf.						
Atavograptus strachani Hutt & Rick.						?						
Monagraptus sp.						●					●	●
Climacagraptus sp.	●					●	●	●				
Lagaragraptus acinaces (Törnq.)						cf.						
Monagr. austerus vulgaris Hutt						●						
Dictyanema carrugatellum Lapw.						?						
Diplagraptus elangatus Churkin & C						aff.						
Pseudaglyptagraptus sp. I. Rick. 1972						?						
Monagraptus revolutus Kurck							cf.					
Managr. triangulatus separatus Sud							?					
Monagr. triangulatus fimbriatus Nich.							?	cf.				
Climacagraptus alternis Packham							?					
P.(Clinoclimacograptus) retroversus B.& R.							●	●	●	●	?	
Monogr. austerus sequens Hutt							●					
G.(Pseudoglyptagraptus) vas B. & R.							?	●				
G. tamariscus linearis (Perner)								cf.				
Rastrites peregrinus Barr.								●				
Orthogr. insectiformis Nich.								●				
Glyptagr. incertus E. & W.								?				
Diplogr. magnus H. Lapw.							?	●				
Petalogr. minar Elles								●				
G. t. tamariscus Nich.								●				
Orthagr. cyperoides Tärnq.								cf.				
indeterminate biserials						●		●		●		
Dictyonema venustus Lapw.										●		
Discograptus sp.										●		
Atavagraptus atavus (Janes)								?				
Karemagraptus sp.								●				
Pristiagraptus regularis (Tärnq.)										cf.		
Orthagraptus sp.										●		
Monagr. convalutus (Hisinger)											aff.	
Orthogr. bellulus											cf.	
Rastrites linnaei											aff.	
Monograptus sedgwickii (Portl.)											●	
Lagaragraptus tenuis (Portl.)												
Managr. runcinatus Lapw.												●
Rhabdopleura sp. nav.												●
chitinous hydraids	●											
P. (Metaclimacograptus) sp.										●		●

Fig. 19 Graptolites found and zones recorded from the type Llandovery area. Each species is recorded at its highest taxonomic level (i.e. 'aff.' rather than '?') when several localities are involved. The text is strictly accurate in its attributions. Graptolite zones in quotation marks indicate that the zonal indicators have not been found, but that other graptolites are present at that approximate level. The black dots indicate specimens found in the appropriate zones in the type Llandovery area.

Table 1 Early Llandovery brachiopods and other faunas from localities in the Scrach section (transect i) in the northern Llandovery area. Counting conventions for this and Tables 2 to 5 are: brachiopods – umbonal fragments only counted; ostracods and bivalves – number of valves; trilobites – numbers of cranidia + pygidia; other groups – numbers of specimens; '×' denotes occurrence of items such as crinoid ossicles where the number of original animals represented is difficult to determine.

Formations	Bronydd				Crychan										
Localities	61a	26	26a	27	224	28c	32	63	186	64	65	34	34a	66	35
Sample mass (kg)	1·9	11·4	5·9	6·8	16·6	3·6	4·2	3·6	4·3	15·7	6·1	11·0	5·7	4·2	2·2
Brachiopods															
Inarticulata indet.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dolerorthis sowerbyiana	–	1	2	–	–	–	1	–	–	2	–	–	–	–	2
Schizonema sp.	–	–	1	5	–	–	–	–	–	–	–	–	–	–	–
Giraldiella sp.	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Skenidioides sp.	1	1	18	–	–	–	–	–	–	4	1	–	–	–	1
indet. orthaceans	–	–	7	11	–	–	–	–	–	1	–	–	–	–	1
Ravozetina sp.	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–
'*Resserella*' sp.	–	3	41	26	–	1	4	1	4	18	10	–	–	–	6
Dicoelosia sp.	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–
Visbyella sp.	–	–	–	–	–	–	–	–	–	–	–	20	–	–	1
indet. enteletaceans	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
Triplesia sp.	1	2	–	–	–	–	–	–	–	1	1	–	–	–	–
Leangella scissa	–	1	29	26	1	–	1	1	3	9	4	–	–	1	3
Anisopleurella sp.	1	5	1	–	–	–	1	–	–	1	–	–	–	–	–
Eoplectodonta duplicata	10	13	28	20	–	1	3	2	2	12	1	–	3	2	8
Katastrophomena sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Leptaena valentia	–	1	3	1	–	–	–	–	1	–	2	–	–	–	1
'*Leptaena*' *reedi*	–	–	1	2	–	–	–	–	–	4	–	–	–	–	–
Eopholidostrophia sp.	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–
Leptostrophia sp.	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–
Fardenia sp.	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–
indet. strophomenides	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Stricklandia lens	–	–	–	–	19	4	1	–	–	1	1	53	25	38	–
Clorinda undata	–	–	–	17	–	–	–	–	–	–	2	–	–	–	–
indet. pentamerids	15	1	–	–	–	–	–	–	–	–	–	2	–	–	–
Rhynchotrema sp.	–	1	1	–	1	–	–	1	–	1	–	–	–	–	–
Protozyga sp.	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–
Plectatrypa sp.	5	3	16	4	–	4	–	–	–	–	1	–	–	–	–
Meifodia sp.	–	–	–	69	17	14	–	–	–	–	1	–	8	–	–
Cryptothyrella angustifrons	33	16	246	41	6	1	–	–	–	–	–	–	–	–	–
Cryptothyrella crassa	–	–	–	14	–	2	–	–	–	1	–	1	–	–	–
indet. spiriferides	1	–	1	8	–	1	–	–	–	–	–	–	–	–	–
indet. articulates	1	1	1	3	1	–	–	–	–	1	1	2	–	–	–
Total brachiopods	69	50	405	251	45	28	11	5	10	60	25	78	36	42	23
Other phyla															
solitary coral	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
compound coral	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Leonaspis sp.	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
other trilobites	–	×	–	–	–	–	–	–	–	–	–	–	–	–	×
graptoloids	–	–	–	–	–	–	–	–	–	1	1	–	–	4	4
gastropods	–	–	22	2	–	–	–	–	–	2	–	1	–	–	1
bivalve	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
crinoid columnals &c.	×	×	×	–	–	–	–	–	–	–	–	–	–	–	×
echinoderm plates	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–
bryozoans	×	–	–	×	–	–	–	–	×	×	–	–	–	–	–
Incertae sedis	–	2	–	–	–	–	–	–	2	–	2	–	–	–	2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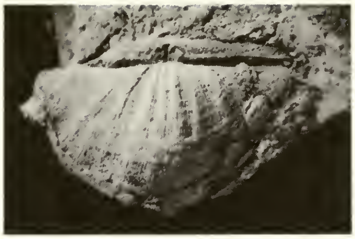
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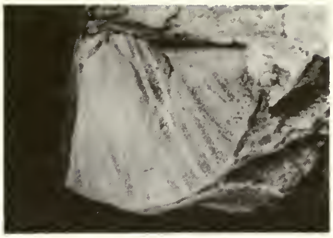
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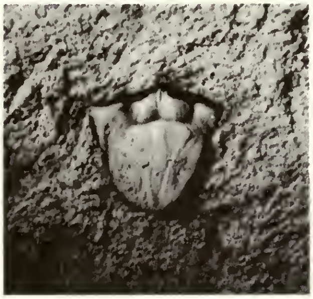
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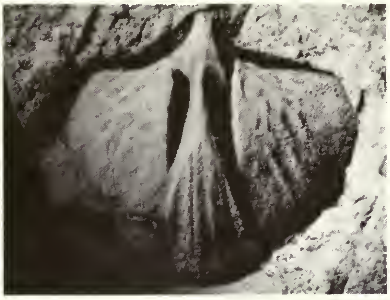
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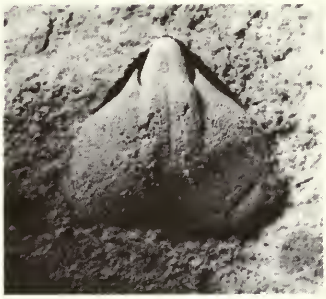
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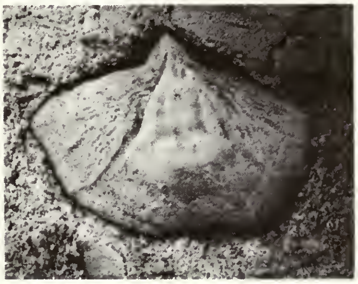
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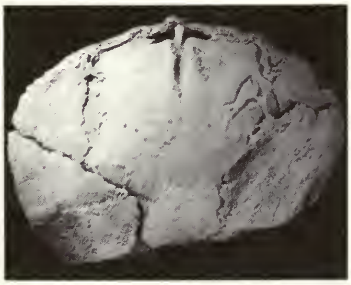
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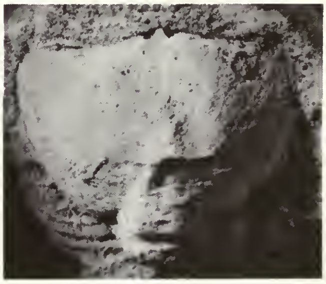
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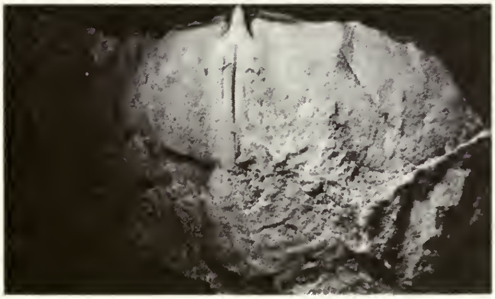

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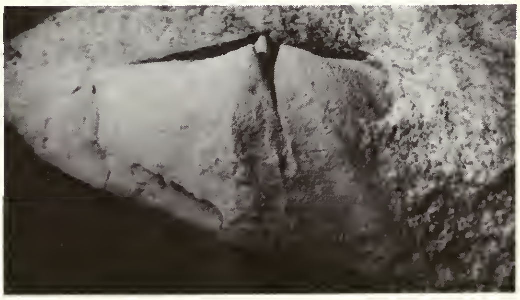


Figs 20–30 Brachiopods from the Rhuddanian Stage (BB, British Museum (Natural History) specimens). Figs 20–22, *Eoplectodonta duplicata* (J. de C. Sowerby, 1839), Goleugoed Formation; Fig. 20, internal mould of pedicle valve, BB 68640, ×2, Loc. 180; Fig. 21, external mould of brachial valve, BB 68641, ×2·5, Loc. 214; Fig. 22, internal mould of pedicle valve, GSM Geol. Soc. Coll. 6874, lectotype, ×2, locality 'Cefn Rhyddan'. Fig. 23, *Leangella scissa* (Davidson, 1871), internal mould of pedicle valve; BB 68647, ×2; Goleugoed Formation, Loc. 180. Fig. 24, *Cryptothyrella crassa* (J. de C. Sowerby, 1839), internal mould of pedicle valve, GSM Geol. Soc. Coll. 6901, lectotype, ×2, Goleugoed Formation, locality 'Cefn Rhyddan'. Fig. 25, *Cryptothyrella angustifrons* (Salter, 1851), internal mould of pedicle valve; BB 68644, ×4; Bronydd Formation, Loc. 26A. Figs 26–28, *Meifodia subundata* (M'Coy, 1851), Bronydd Formation, Loc. 27; Fig. 26, internal mould of pedicle valve, BB 68648, ×2; Figs 27, 28, internal moulds of brachial valves, BB 68646 and BB 68645, both ×2. Figs 29–30, *Stricklandia lens* (J. de C. Sowerby, 1839), Loc. 97A; Fig. 29, internal mould of brachial valve, BB 68643, ×2; Fig. 30, internal mould of pedicle valve, BB 68642, ×2.

Table 2 Early Llandovery brachiopods and other faunas from localities in the Trefawr section (transect h), which includes the basal stratotype of the Aeronian Stage in the northern Llandovery area.

Formations	Crychan	Trefawr														
Localities	41a	38s	38a	70	70a	38b	71	72	73	74	75	38c1	38c	39	39a	76
Sample mass (kg)	4·5	2·2	2·0	4·2	4·0	2·3	4·4	4·5	5·5	7·1	3·5	–	11·7	2·4	2·5	3·6
Brachiopods																
discinids	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
craniids	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
indet. inarticulates	–	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Dolerorthis sowerbyiana	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1
Dolerorthis sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Skenidioides sp.	1	–	–	7	6	–	1	4	1	7	3	–	4	–	–	–
'Resserella' sp.	2	–	1	10	4	1	–	–	–	2	3	–	9	–	–	3
Dicoelosia sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Triplesia sp.	–	–	–	–	–	–	1	2	–	–	1	1	–	–	5	1
Streptis sp.	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
Leangella scissa	2	–	–	–	10	5	1	–	3	5	7	–	5	–	–	1
Anisopleurella sp.	–	–	–	–	5	5	–	1	6	1	–	–	7	–	–	–
Eoplectodonta duplicata	2	4	–	–	7	3	–	–	–	4	1	–	7	2	–	–
Aegiria sp.	–	–	6	–	–	–	–	–	2	4	–	–	–	–	–	–
Katastrophomena sp.	1	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Leptaena valentia	–	–	–	–	–	–	–	–	1	–	–	–	3	1	–	–
'Leptaena' reedi	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–
Pentlandina sp.	–	–	–	–	1	–	–	–	6	6	–	–	–	–	–	–
Eopholidostrophia sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
indet. strophomenides	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Stricklandia lens	22	–	–	–	1	–	1	–	–	3	2	3	–	–	1	3
Clorinda undata	–	–	–	–	–	1	7	8	1	–	1	–	14	6	9	17
Rhynchotrema sp.	–	–	–	–	2	–	–	1	–	–	–	–	20	7	–	–
Plectatrypa sp.	–	10	–	–	2	–	5	3	–	–	–	–	8	9	–	22
Meifodia sp.	–	–	1	–	–	–	–	1	13	20	2	6	16	10	37	15
Cryptothyrella crassa	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
indet. spiriferides	1	–	2	–	2	–	–	–	7	8	2	–	–	–	2	1
indet. articulates	3	–	–	2	–	1	3	1	1	–	1	–	–	–	–	–
Total brachiopods	35	18	11	20	42	17	19	21	42	60	23	11	95	36	55	66
Other phyla																
solitary corals	–	–	–	–	1	–	–	1	–	–	–	–	1	–	–	–
illaenid trilobites	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
calymenid trilobites	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
other trilobites	–	–	–	–	×	×	–	×	–	–	–	–	–	–	–	–
ostracods	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–
graptoloids	–	2	–	2	2	–	–	–	8	–	11	–	3	–	–	–
dendroid	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
gastropods	–	–	–	2	–	–	–	1	1	1	–	–	–	–	–	–
cephalopod	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
crinoid columnals &c.	–	–	–	–	–	×	–	–	–	×	×	–	×	–	–	–
echinoderm plates	–	2	2	–	–	–	1	–	1	1	–	–	–	–	–	–
bryozoans	×	–	–	–	–	×	–	×	–	–	–	–	×	–	–	×
Incertae sedis	–	–	–	–	–	1	–	2	–	–	–	–	1	–	–	–

Table 3 Early Llandovery brachiopods and other faunas from localities in the Cwm-coed-aeron section (transect i) in the northern Llandovery area.

Formations	Trefawr													Rhydings	
Localities	211	212a	212	67	209	208	207	201	202	203	204	205	206	138	137a
Sample mass (kg)	4·5	2·0	4·6	8·7	4·6	8·6	2·2	5·0	5·0	4·7	9·9	7·5	5·2	8·1	8·5
Brachiopods															
lingulacean	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–
Paracraniops sp.	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–
Dolerorthis sowerbyiana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Schizonema sp.	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–
Giraldiella sp.	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
indet. orthaceans	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–
Ravozetina sp.	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–
'Resserella' sp.	–	–	–	–	–	–	–	–	–	–	9	2	–	1	1
Dicoelosia sp.	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–
Triplesia sp.	–	–	–	–	–	–	–	–	–	–	1	–	–	–	4
Eoplectodonta sp.	–	–	–	–	–	1	–	–	–	–	9	14	–	–	2
Katastrophomena sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2
Leptaena valentia	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Stricklandia lens	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Clorinda undata	–	–	1	4	–	–	1	–	–	1	9	62	–	–	–
Pentamerus sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Rhynchotrema sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Plectatrypa sp.	1	–	–	–	4	8	–	4	–	–	1	6	–	–	1
Meifodia sp.	6	4	–	5	3	14	1	7	2	1	21	36	10	3	1
indet. spiriferides	7	–	1	3	–	–	–	–	–	–	–	2	–	–	1
indet. articulates	–	–	–	1	–	–	–	–	–	–	3	2	–	–	–
Total brachiopods	14	4	2	17	7	23	2	13	3	2	66	127	10	6	13
Other phyla															
echinoderm plates	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
bryozoans	–	–	–	–	–	–	–	–	–	–	×	×	–	–	–
Incertae sedis	–	–	1	–	–	–	–	1	–	–	1	–	–	–	–

(b) Brachiopods from the lower part of the series (pre-Rhydings Formation)
Brachiopods form the dominant elements of the shelly faunas in both the northern and southern areas. In the northern area a total of 1978 brachiopods have been collected from 47 sites (mean sample size 42·1), and in the southern area 1277 brachiopods from 12 sites (mean sample size 106·4). The difference in numbers of sites reflects the more continuous exposures in the north, which lend themselves to closely-spaced sampling.

Plots of number of recorded species against size of sample reveal no evidence of differences in overall diversity of brachiopod faunas between the northern and southern areas. There are, however, more taxa which have been found only in the north (10) than only in the south (2), and although most of these are rare forms whose absence can probably be attributed to defects of sampling, there are four taxa whose absence from the south may be more significant – *Aegiria, Cryptothyrella angustifrons, Pentlandina* and *'Leptaena' reedi*. The first three of these are found in the Garth area a few km to the north of the northern area, while *'Leptaena' reedi* is otherwise unknown in early Llandovery strata anywhere south of the Berwyn outcrop.

The early Llandovery brachiopods do not form well-defined assemblages or 'communities', with the exception of *Stricklandia*-dominated assemblages which occur in the middle parts of the successions in both areas – Locs 97b–183 in the south, and Locs 34–66 (including 41a) in the north. These *Stricklandia*-dominated assemblages show extremely low diversity (and high

Table 4 Early Llandovery brachiopods and other faunas from localities in the Ydw Valley (transect c) in the southern Llandovery area.

Formations	Goleugoed											
Localities	150	178	179	97b	97a	180	98	181	182	183	184	120
Sample mass (kg)	6·0	–	18·7	–	–	19·8	–	3·6	2·3	–	12·6	–
Brachiopods												
lingulacean	–	–	1	–	–	–	–	–	–	–	–	–
Dolerorthis sowerbyiana	–	1	–	–	–	–	–	–	–	–	1	6
Schizonema sp.	–	1	1	2	–	1	–	–	–	–	–	2
Giraldiella sp.	–	1	–	–	–	–	–	–	–	–	–	2
Skenidioides sp.	–	2	1	4	–	10	–	–	–	1	–	2
indet. orthaceans	–	1	–	–	1	1	–	–	–	–	–	–
Ravozetina sp.	–	–	–	–	–	3	–	–	–	–	1	1
'Resserella' sp.	1	11	8	17	8	45	2	2	2	–	2	9
Dicoelosia sp.	–	2	–	–	–	–	–	–	–	–	–	–
Visbyella sp.	–	–	2	–	1	4	–	–	–	–	–	–
Saukrodictya sp.	–	–	–	–	1	–	–	–	–	–	–	–
indet. enteletaceans	–	–	–	–	–	1	–	–	–	–	3	–
Triplesia sp.	–	–	–	–	–	2	–	–	–	–	3	2
Leangella scissa	–	20	5	26	13	62	–	2	3	6	3	20
Anisopleurella sp.	3	–	–	–	–	3	–	–	–	–	–	15
Eoplectodonta duplicata	1	26	3	13	8	66	–	1	3	2	2	26
Katastrophomena sp.	–	3	–	1	–	–	–	–	–	–	–	2
Leptaena valentia	–	2	–	–	–	1	–	–	–	–	–	15
Eopholidostrophia sp.	–	2	–	–	–	–	–	–	–	–	–	2
Leptostrophia sp.	–	–	–	–	–	–	–	–	–	–	–	1
Eostrophonella sp.	–	–	–	–	–	1	–	–	–	–	–	–
Fardenia sp.	–	2	–	1	–	1	–	–	–	–	–	–
Stricklandia lens	1	12	2	79	71	6	–	84	3	108	5	2
Clorinda undata	–	–	–	2	2	2	–	1	–	–	10	24
indet. pentamerides	–	–	–	1	8	–	36	–	–	–	1	4
Rhynchotrema sp.	–	2	–	–	–	3	–	–	–	–	3	7
Plectatrypa sp.	–	2	2	3	–	2	–	1	–	1	10	35
Meifodia sp.	–	5	–	–	1	2	1	1	2	–	19	92
Cryptothyrella crassa	–	21	–	2	–	–	–	–	–	–	–	–
indet. spiriferides	–	–	–	–	–	–	–	–	–	–	–	14
indet. articulates	–	8	3	9	3	7	–	–	1	–	1	8
Total brachiopods	6	124	28	160	117	223	39	92	14	118	64	292
Other phyla												
solitary corals	–	–	1	–	–	3	–	–	–	–	–	1
compound coral	1	–	–	–	–	–	–	–	–	–	–	–
illaenid trilobites	–	2	–	–	–	–	–	–	–	–	–	–
calymenid trilobites	–	–	–	–	–	2	–	–	–	–	–	–
Encrinurus sp.	–	1	–	–	–	–	–	–	–	–	–	–
Leonaspis sp.	–	–	–	–	–	–	–	–	–	1	–	–
other trilobites	×	–	–	–	–	–	–	–	–	–	–	×
graptoloids	–	–	2	–	–	1	–	–	–	–	–	1
gastropods	–	–	2	3	–	–	–	–	–	–	–	–
cephalopod	–	–	–	–	–	1	–	–	–	–	–	–
crinoid columnals &c.	×	–	×	×	–	×	–	–	×	–	–	–
echinoderm plate	–	–	–	–	–	1	–	–	–	–	–	–
bryozoans	×	×	–	×	–	×	–	–	×	×	–	×
Incertae sedis	1	–	–	–	–	1	–	–	–	–	–	–

dominance) compared with assemblages dominated (relatively weakly) by '*Resserella*', *Eoplectodonta* (Figs 20–22) or *Meifodia* (Figs 26–28): contrast, for instance, Loc. 183 with Loc. 178 in the south, and Loc. 34a with Loc. 64 in the north (Tables 1–4).

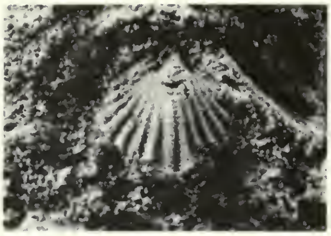
The sequences of early Llandovery brachiopod faunas in the south and north have been slotted into each other, using the program developed by Gordon (1980). Results of this slotting suggest that the lowest part of the northern section, the Bronydd and lower Crychan Formations (Loc. 61a up to around Loc. 62), is earlier than the lowest abundant sample (Loc. 178) from Ydw Valley, and this part of the northern section is therefore represented by largely unfossiliferous strata in the south. From this horizon upwards, i.e. within the upper part of the Crychan and Trefawr Formations in the north and within the upper part of the Goleugoed Formation in the south, the sequence of early Llandovery brachiopod faunas in the two areas is roughly parallel, although with local reversions and intercalations: '*Resserella*'- and *Eoplectodonta*-dominated assemblages are followed by assemblages (well represented in the south) strongly dominated by *Stricklandia*, and then by *Meifodia*- and *Plectatrypa*-dominated assemblages. These parallel changes in the composition of the brachiopod faunas presumably reflect parallel changes in the environment in the northern and southern areas during the upper part of the early Llandovery. Detailed systematic work on the early Llandovery brachiopod faunas is still proceeding. The taxa listed on Tables 1–4 are mostly interpreted in the sense of Temple (1970).

(c) Brachiopods from the upper part of the series (Rhydings Formation upwards)

Brachiopods can be found at most upper Llandovery outcrops in all parts of the area and some representative collections are shown in Table 5. These collections, from the southern part of the area, are larger than those (unlisted here) from the north of the Llandovery area, and reflect a genuinely greater abundance and diversity in the south: the reverse of the situation in the Lower Llandovery. The most important section of late Llandovery age is that of the Cefn Cerig Road (transect d of Fig. 4), where almost continuous exposure extends through the Rhydings, Wormwood and lower part of the Cerig Formations and which includes (near the top of the Wormwood Formation) the type locality of the base of our revised Telychian Stage.

As can be seen from Table 5, the brachiopod faunas do not change greatly at the generic level during this period, apart from the local incoming of eospiriferids near the top of the Rhydings Formation and *Pentlandella* near the end of Llandovery time. However, the changes of most importance occur at the subgeneric, specific and subspecific levels. Two genera are paramount in these evolutionary studies: the pentameride *Stricklandia* and the rhynchonellide *Eocoelia*. In the Lower Llandovery *Stricklandia lens prima, S. lens lens* and *S.lens intermedia* are found (Williams 1951); in the Rhydings Formation and the Wormwood Formation *S. lens progressa* can be abundant, and in the Cerig Formation (e.g. at Loc. 163), the species *laevis* (previously known as *S. lens ultima*), which shows incipient ribbing, occurs. This stricklandiid lineage has been the subject of intense work since its original description by Williams (1951), and has been independently validated from Estonia (Rubel' 1977), Norway (Baarli & Johnson 1982), the U.S.A. (Amsden 1966, Johnson 1979): it is also known from many other areas in Britain and elsewhere.

Whilst *Stricklandia* is a very common fossil in the type Llandovery area, even finer subdivision may be achieved by the analysis of *Eocoelia*. Although Ziegler (1966) divided *Eocoelia* into successive species (of which *hemisphaerica* and *intermedia* occur in the Aeronian Stage, *curtisi* and *sulcata* in the Telychian Stage and *angelini* in the lower Wenlock Sheinwoodian Stage), in fact there is a progressive gradation in the stock in which both the ribbing characteristics and the articulation morphology change gradually with time; thus the species have arbitrarily-defined boundaries within a continuous spectrum. Fortunately, as recorded in Ziegler (1966: 530, 536) and confirmed by our recent collecting, *Eocoelia* is present in several localities in the type Llandovery area, and the progression from *E. hemisphaerica* through *E. intermedia* to *E. curtisi* can be traced in the southern part of the area in continuous sections with simple stratigraphy.



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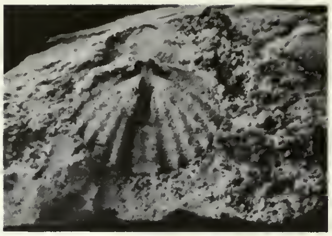

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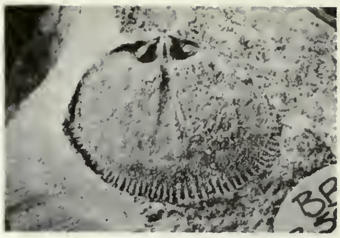

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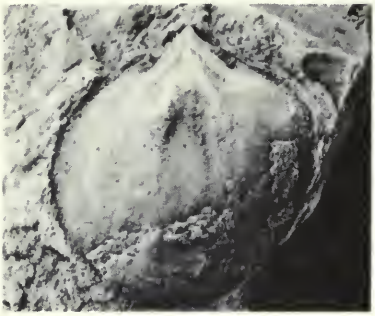

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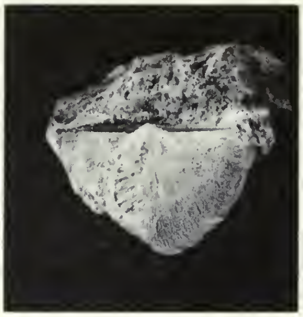

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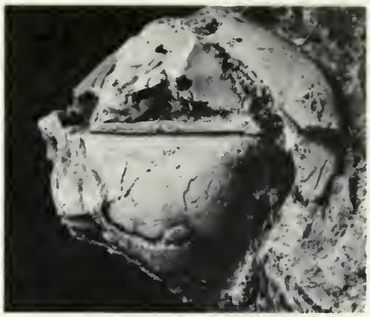

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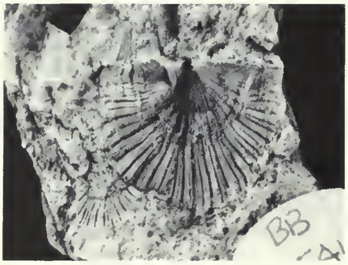

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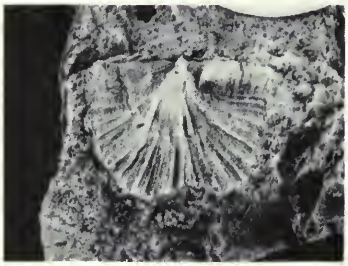

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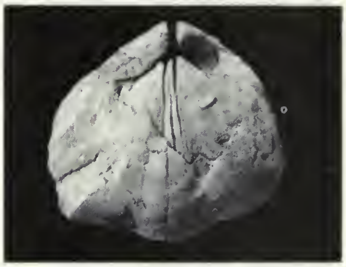

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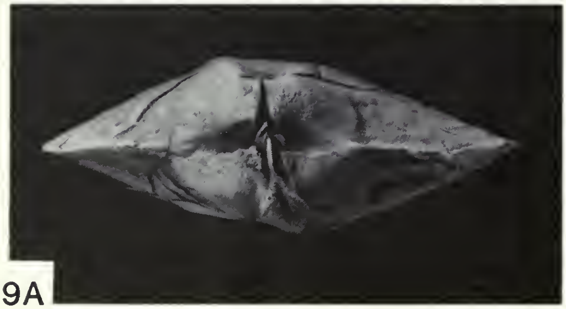

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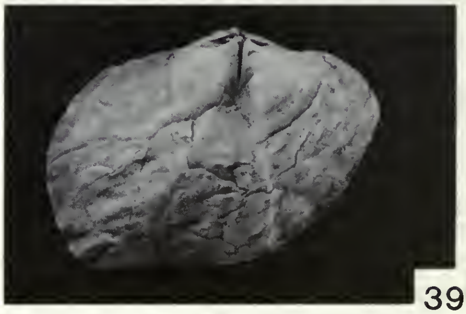
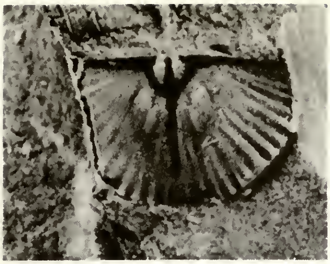


39B

Figs 31–39 Brachiopods from the Aeronian Stage. Figs 31, 32, *Eocoelia intermedia* (Hall, 1860), Wormwood Formation; Fig. 31, internal mould of pedicle valve, BB 65426, ×3, Loc. 162; Fig. 32, internal mould of brachial valve, BB 38447, ×3, Loc. 170. Fig. 33, *Mendacella polygramma* (J. de C. Sowerby, 1839), internal mould of brachial valve; BB 35997, ×2; Rhydings Formation, Loc. 157. Fig. 34, *Glassia* aff. *tenella* Williams, 1951, internal mould of pedicle valve; BB 93861, ×3; Rhydings Formation, Loc. 109. Figs 35, 36, *Eopholidostrophia sefinensis* (Williams, 1951), Rhydings Formation, Loc. 169; Fig. 35, internal mould of pedicle valve, BB 93785, ×2; Fig. 36, external mould of conjoined valves, BB 95755, ×2. Fig. 37A, B, *Leptostrophia tenuis* Williams, 1951, respectively external and internal moulds of pedicle valve; BB 34541, ×2; Rhydings Formation, Loc. 169. Fig. 38, *Pentamerus oblongus* J. de C. Sowerby, 1839, internal mould of conjoined valves; BB 68565, ×1; Rhydings Formation, Loc. 14. Fig. 39A, B, *Stricklandia lens progressa* Williams, 1951, posterior and pedicle views respectively of internal mould of conjoined valves; B 5614, ×1·5 and ×1; Rhydings Formation, Loc. 168.



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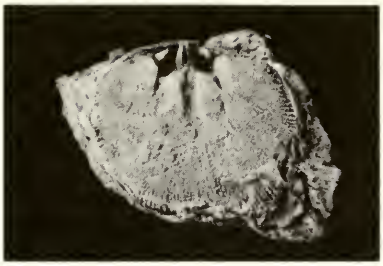

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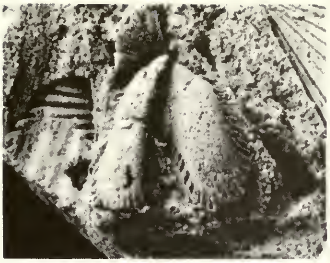

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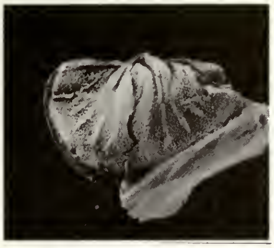

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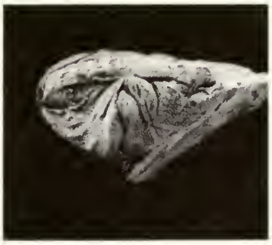

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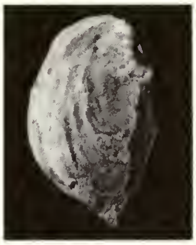

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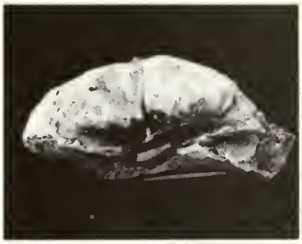

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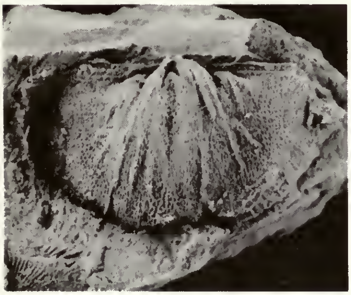

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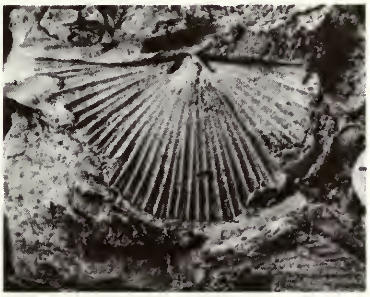

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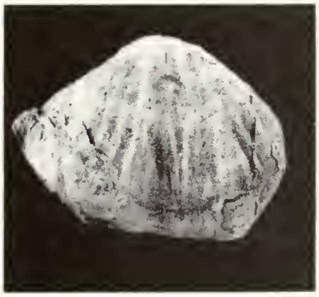

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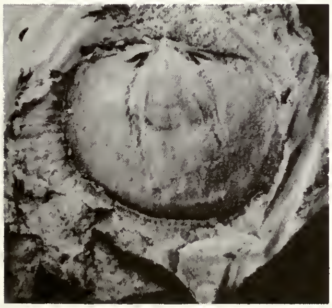

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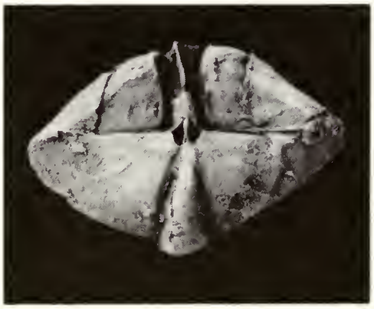

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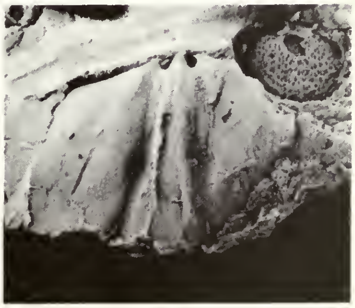

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Figs 40–49 Brachiopods from the Telychian Stage. All those illustrated come from the Cerig Formation, Loc. 163. Fig. 40, *Skenidioides lewisii* (Davidson, 1848), internal mould of brachial valve; BB 72818, ×4. Fig. 41, *Isorthis mackenziei* Boucot, Johnson, Harper & Walmsley, 1966, internal mould of brachial valve; BB 72767, ×2. Fig. 42, *Dicoelosia alticavata* (Whittard & Barker, 1950), internal mould of pedicle valve; BB 72786, ×3. Figs 43A, B, 45, *Eoplectodonta penkillensis* (Reed, 1917), internal moulds of pedicle valves; Figs 43A, B, BB 31776, ×2; Fig. 45, BB 31803, ×2·5. Figs 44A–C, *Clorinda globosa* (J. de C. Sowerby, 1839), internal mould of pedicle valve viewed laterally, posteriorly and from above; BB 73032, ×2. Fig. 46, *Coolinia applanata* (Salter, 1846), internal mould of pedicle valve; BB 72963, ×2. Fig. 47, *Atrypa orbicularis* J. de C. Sowerby, 1839, internal mould of pedicle valve; BB 72871, ×2. Figs 48, 49, *Eospirifer* aff. *radiatus* (J. de C. Sowerby, 1834); Fig. 48, internal mould of conjoined valves, BB 72927, ×2; Fig. 49, internal mould of brachial valve, BB 72908, ×3.

Table 5 Later Llandovery brachiopods and other macrofaunas from localities in the southern part of the Llandovery area.'××' denotes the abundant occurrence of crinoidal debris.

Formations	Rhydings					Wormwood				Cerig
Localities	168	169	109	156	157	170	161	162	187	163
Brachiopods										
Lingula spp.	–	6	–	–	–	–	–	–	–	1
Craniops implicatus	–	1	–	1	–	1	–	–	–	56
Orbiculoidea sp.	–	3	–	–	–	–	1	–	–	–
Dolerorthis psygma	2	–	–	–	–	11	1	1	–	–
Hesperorthis sp.	–	–	–	2	–	7	–	–	–	3
Giraldiella protensa	–	47	–	–	–	1	–	–	–	–
Skenidioides lewisii	1	–	–	1	1	14	8	2	39	80
indet. orthaceans	–	1	–	1	–	–	–	–	–	–
Isorthis beechhillensis	15	34	–	–	–	–	–	–	–	–
Isorthis mackenziei	–	–	–	–	–	–	–	–	17	7
Isorthis sp.	–	–	–	18	7	18	7	–	–	–
Resserella sefinensis	6	23	–	–	–	–	–	–	–	–
Resserella sp.	–	–	32	22	15	55	12	13	–	53
Visbyella pygmaea	–	2	–	–	–	–	–	–	42	17
Mendacella sp.	–	–	–	–	1	–	–	1	–	–
Dicoelosia alticavata	–	–	–	46	114	–	10	–	17	80
Triplesia sp.	2	–	–	–	–	1	–	–	–	–
Streptis sp.	–	–	–	–	–	–	–	–	–	5
Leangella scissa	2	26	6	–	1	–	–	–	–	–
Leangella segmentum	–	–	–	–	–	65	30	7	43	–
Eoplectodonta penkillensis	–	14	34	–	6	133	63	20	77	232
Ygerodiscus undulatus	3	–	–	2	–	–	–	–	–	–
Aegiria grayi	–	–	10	10	20	21	–	–	5	–
Katastrophomena penkillensis	1	1	–	1	1	–	2	1	1	–
Pentlandina parva	–	–	–	–	–	–	2	–	–	5
Leptaena purpurea	–	–	–	1	–	3	1	–	–	17
Leptaena urbana	–	–	–	–	–	–	–	1	3	–
Leptaena valida	–	11	–	–	–	–	–	–	–	–
Leptaena sp.	–	–	1	–	1	–	–	–	–	–
Cyphomenoidea wisgoriensis	–	–	–	–	–	1	–	–	–	–
Eostropheodonta sp.	–	2	–	1	–	–	–	–	–	–
Leptostrophia compressa	–	–	–	–	–	2	–	–	–	17
Leptostrophia tenuis	–	130	–	–	–	–	–	–	–	–
Eopholidostrophia sefinensis	–	177	–	–	–	–	–	–	–	–
Mesopholidostrophia salopiensis	–	–	1	5	6	4	5	3	3	49
Coolinia applanata	–	5	–	–	–	79	1	12	5	82
Parastrophinella? sp.	–	–	–	1	–	1	–	–	–	–
Stricklandia laevis	–	–	–	–	–	–	–	–	–	1
Stricklandia lens progressa	168	–	–	–	6	9	1	2	–	–
Pentamerus oblongus	–	–	–	–	–	21	–	7	1	–
Clorinda globosa	–	–	11	–	1	54	4	10	13	332
Rostricellula? sp.	–	1	–	–	–	–	–	–	–	–
Stegerhynchus sp.	–	1	–	–	–	8	–	–	–	–
Sphaerirhynchia sp.	–	–	–	–	–	–	–	–	–	2
Eocoelia hemisphaerica	–	43	–	–	–	–	–	–	–	–
Eocoelia intermedia	–	–	–	–	2	11	3	2	–	–
Eocoelia curtisi	–	–	–	–	–	–	–	–	–	3
Pentlandella pentlandica	–	–	–	–	–	–	–	–	1	2
Atrypa orbicularis	–	–	1	4	–	32	1	5	5	113
Protatrypa sp.	–	–	–	–	1	–	–	–	–	12
Eospirigerina sp.	–	5	–	–	–	–	–	–	–	–

Table 5 – *continued*

Formations	Rhydings					Wormwood				Cerig
Localities	168	169	109	156	157	170	161	162	187	163
Glassia? sp.	–	–	22	5	2	13	5	–	4	31
Meifodia ovalis	–	1	–	–	–	–	1	–	–	–
Eospirifer aff. *radiatus*	–	–	–	8	–	–	–	2	2	93
Cyrtia aff. *exporrecta*	–	–	–	–	–	–	–	1	–	–
Total brachiopods	200	534	118	129	173	565	158	90	278	1293
Other phyla										
illaenid trilobite	–	–	–	–	–	–	1	–	–	–
encrinurid trilobites	–	–	–	–	–	9	5	1	5	2
odontopleurid trilobites	–	2	–	–	–	1	1	1	1	1
calymenid trilobites	–	4	–	1	–	2	–	1	–	–
other trilobites	–	–	–	–	1	–	–	–	4	–
heliolitid coral	–	–	–	–	–	–	–	1	–	–
halysitid corals	–	–	–	–	–	2	1	–	4	–
favositid corals	–	–	–	–	–	35	–	–	–	8
streptelasmatid corals	3	–	–	1	1	34	9	12	8	–
halloporan bryozoans	1	1	1	4	3	1	–	2	1	6
thin twig bryozoans	–	–	–	1	1	2	2	–	2	–
net bryozoans	–	–	–	1	1	–	–	–	3	1
encrusting bryozoans	–	–	–	–	–	8	–	–	1	11
bellerophont mollusc	–	1	–	–	–	–	–	–	–	–
various gastropods	–	8	–	2	1	1	1	–	–	1
various bivalves	–	–	–	–	–	–	–	–	1	1
orthoceratid cephalopod	–	–	–	–	–	–	–	–	1	–
'*Tentaculites*'	–	11	–	–	1	1	–	–	–	–
crinoid columnals &c.	–	××	–	–	×	××	××	××	×	××

In addition, the *Borealis–Pentamerus–Pentameroides* lineages (e.g. Mørk 1981, Baarli & Johnson 1982), the lineages of *Leptostrophia compressa* and other leptostrophiids (Cocks 1967), pholidostrophiines (Hurst 1974) and atrypides (e.g. Copper 1982) can be useful in correlation and local dating. All these forms are present in the type Llandovery at Llandovery, and some are included in the summary chart at the end of this paper (Fig. 69). Species authors can be found in Cocks (1978).

Other brachiopods recorded from the late Llandovery of Llandovery, but not found in the collections shown in Table 5, are *Lingula pseudoparallela, Lingula symondsii, Schizocrania* sp., *Philhedrella* sp., *Triplesia anticostiensis, Triplesia glabra, Brachyprion arenacea, Strophonella* (*Eostrophonella*) *davidsoni, Amphistrophia whittardi, Fardenia* sp., *Antirhynchonella* sp., *Stegerhynchus*? *neglectus, Stegerhynchus weaveri, Whitfieldella* sp., *Hindella*? *furcata, Atrypina* sp. and *Howellella anglica*. Other species are undoubtedly present, particularly of enteletaceans, rhynchonellids and atrypoids, but further taxonomic research is needed before they can be identified satisfactorily.

When analysing the ecology, the communities proposed by Ziegler, Cocks & Bambach (1968) can be identified in most of the late Llandovery assemblages. In general the base of the Rhydings Formation carries *Stricklandia* assemblages (including the type locality for *Stricklandia lens progressa*), but the beds above this in the Rhydings Formation yield progressively deeper-water faunas with *Clorinda* and its assemblage, until at about the Rhydings–Wormwood boundary the deepest-water shelly assemblages are reached, which include such forms as *Aegiria* and *Dicoelosia* as well as less common *Clorinda*. Higher in the Wormwood Formation there is a progressive shallowing to *Stricklandia* and *Pentamerus*

Community assemblages, but the top of the Wormwood Formation and the Cerig Formation show renewed deepening, with *Clorinda* Community assemblages and even deeper-water faunas with only occasional shelly fossils in the upper part of the Cerig Formation. Superimposed on this pattern is a relative shallowing to the assumed land areas to the south-east from the basin to the north-west, so that, for example, the later Llandovery Derwyddon Formation of the Pen-y-waun fault belt carries shallower-water assemblages than the contemporary Wormwood Formation at Crychan Forest (transect f on Fig. 4).

(d) Trilobites

Trilobite remains have been found in all of the newly-recognized formations except the Derwyddon Formation. This formation is only locally developed; the apparent absence of trilobites in it may be due to disarticulation and breakage of exoskeletons in the high energy conditions under which it was deposited.

The trilobites are almost always disarticulated. A few complete or nearly complete exoskeletons are known: two specimens of *Diacalymene* (one each from the basal part of the Coldbrook Formation and from the lower part of the Goleugoed Formation), near complete *Calymene, Encrinurus* and *Astroproetus* and an articulated anterior portion of a zeliskellinid from the upper part of the Rhydings Formation, and articulated *Stenopareia* from the Wormwood Formation. The remains are invariably preserved as internal and external moulds. The state of preservation varies greatly; it is usually adequate and sometimes excellent.

Twenty genera of trilobites are represented in collections made during the present work and the older collections – mainly the O. T. Jones Collection (Sedgwick Museum, Cambridge). Of these twenty, calymenids and *Encrinurus* in particular, with *Leonaspis* and *Acernaspis*, dominate numerically. The dominance of these forms is entirely what would be expected in the relatively shallow, inshore marine conditions in which these mainly clastic rocks were deposited. But few specific determinations have yet been made. It is hoped that in particular the material of *Leonaspis* and *Acernaspis* may provide correlations within the area, and possibly outside. Species of these two genera are well known in the Llandovery of Scotland, Scandinavia and Estonia. In the literature a few taxa have been described from the type Llandovery area.

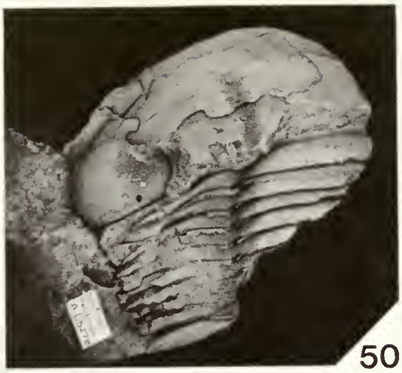
The following list is of the species identified from our new formations.

Bronydd Formation. *Acernaspis* sp., *Diacalymene* sp., *Proetus* (*s.l.*) sp., *Platylichas*? sp.

Crychan Formation. *Acernaspis* sp., *Calymene* sp., *Encrinurus* sp., *Leonaspis* sp., *Stenopareia* sp.

Trefawr Formation. *Acernaspis* sp., *Calymene* sp., *Harpidella* sp., *Leonaspis* sp. (Fig. 55), *Proetus* (*s.l.*) sp.

Figs 50–58 Trilobites from the type Llandovery area (SM = Sedgwick Museum, Cambridge; NMW = National Museum of Wales). Fig. 50, *Stenopareia* sp., dorsal view of cephalon, thorax and fragment of pygidium, internal mould; SM A65278, ×0·6; Rhydings Formation, Loc. 169. Fig. 51, *Stenopareia* cf. *catathema* Howells, 1982, internal mould of thorax and pygidium; SM A65724, ×0·6; Wormwood Formation, Loc. 213. Fig. 52A–D, *Diacalymene* aff. *marginata* Shirley, 1936, palpebral, dorsal, pygidial and left lateral views respectively of complete internal mould; BM(NH) It.18900, ×1; Goleugoed Formation, Loc. 147. Figs 53A, B, 54, *Encrinurus* cf. *mullochensis* Reed, 1931, Rhydings Formation, Loc. 169; Fig. 53A, B, anterior and palpebral views of internal mould of cephalon; NMW 83.37G.1, ×2; Fig. 54, dorsal view of internal mould of thorax and pygidium, SM A65275, ×2. Fig. 55A, B, *Leonaspis* sp., dorsal views of internal mould of cranidium and thorax; SM A66106, ×2; Trefawr Formation, Loc. 114. Fig. 56A–C, *Calymene replicata* Shirley, 1936, dorsal, pygidial and left lateral views of complete internal mould; NMW 83.37G.2, ×2; Rhydings Formation, Loc. 169. Fig. 57, *Decoroproetus* sp. 2 of Owens (1973: 54), dorsal view of latex cast of external mould of complete specimen; SM A81488, ×3; Rhydings Formation, Loc. 169. Fig. 58, *Leonaspis* sp., dorsal view of internal mould of pygidium; NMW 83.37G.3, ×4; Rhydings Formation, Loc. 104.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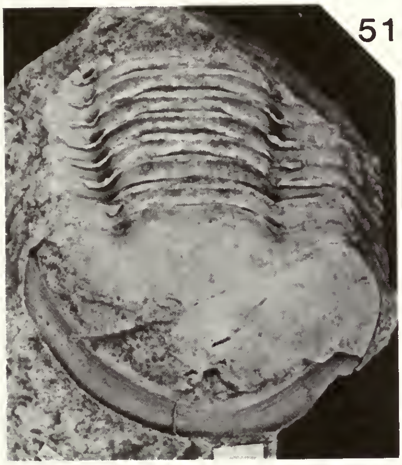
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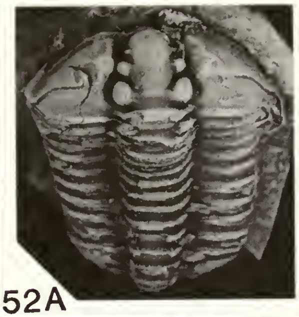
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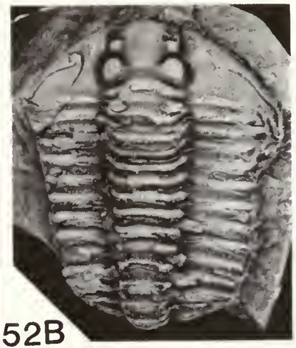
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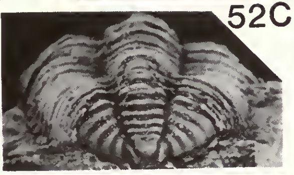
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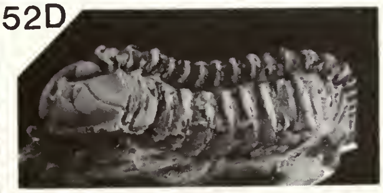
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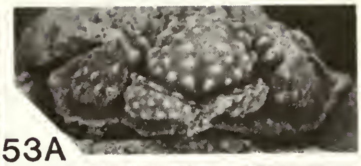
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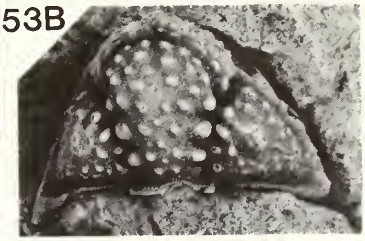
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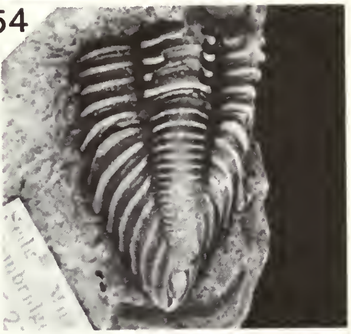
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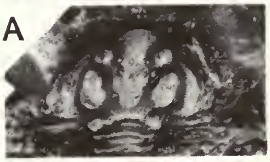
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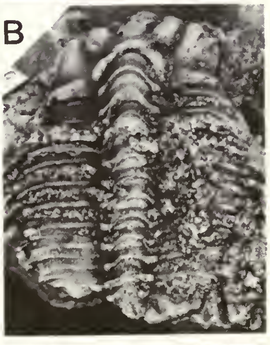
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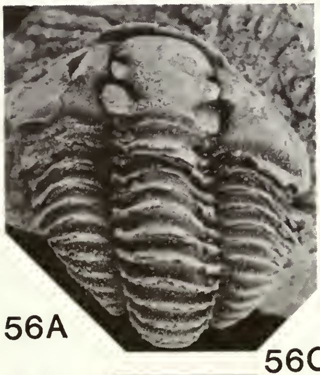
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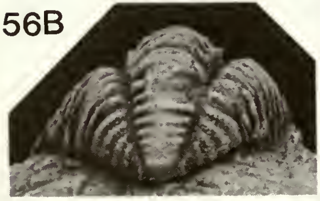
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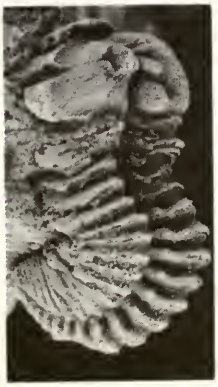
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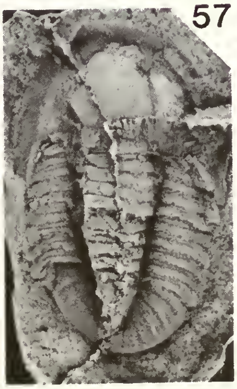
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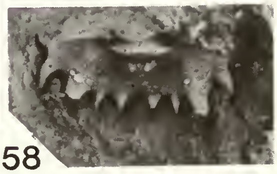
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Coldbrook Formation. *Acernaspis* sp., *Encrinurus* sp., *Leonaspis* sp., *Diacalymene* aff. *marginata* Shirley.

Goleugoed Formation. *Diacalymene* aff. *marginata* Shirley (Fig. 52), *Encrinurus* sp., *Hadromeros*? sp., *Homalonotus* sp.

Rhydings Formation. *Acaste* sp., *Acernaspis* sp., *Astroproetus* aff. *scoticus* (Reed), *Encrinurus* cf. *mullochensis* Reed (Figs 53, 54), *Calymene replicata* Shirley (Fig. 56), *Decoroproetus* sp. 2 of Owens (1973: 54), *Hadromeros* cf. *elongatus* (Reed), *Homalonotus* sp., *Kosovopeltis* sp., *Leonaspis* sp. (Fig. 58), *Stenopareia* sp. (Fig. 50), zeliskellinid.

Wormwood Formation. *Acernaspis* sp., *Calymene* sp., *Decoroproetus* sp., *Encrinurus* sp., *Hadromeros* sp., *Leonaspis* sp., *Stenopareia* cf. *catathema* Howells (Fig. 51), zeliskellinid.

Cerig Formation. *Acernaspis* sp., *Calymene* sp., *Cheirurus* sp. A of Lane (1971: 17), '*Dalmanites*' sp., *Hadromeros* sp., *Youngia* sp.

(e) Molluscs

We have identified the following molluscs, with the help of Dr N. J. Morris of the Department of Palaeontology, BM(NH).

Goleugoed Formation. Bellerophontids: *Cyrtolites nodosus llandoveriana* Reed, *Grandostomus* aff. *dilatatus* (J. de C. Sowerby). Gastropods: *Lophospira* sp., *Liospira*? sp., *Gyronema*? sp., *Subulites* aff. *ventricosus* (Hall). Bivalves: *Cleionychia*? *mytilimeris* (Conrad). Cephalopods: *Trocholites planorbiformis* (Conrad), *Trochodictyoceras*? sp.

Bronydd Formation. Bellerophontid: *Kokenospira* sp.

Crychan Formation. Bellerophontid: *Cyrtolites* sp. Gastropods: *Gyronema octavia* (d'Orbigny, *sensu* Donald), *Lophospira* sp., gosseletininid. Cephalopod: *Trochoceras cornuariete* (J. de C. Sowerby).

Trefawr Formation. Bellerophontid: *Tropidodiscus* sp. Gastropods: *Loxonema*? sp., *Lophospira* sp. Pteriniid bivalve.

Rhydings Formation. Bellerophontids: *Grandostomus* sp., *Tropidodiscus* sp. Gastropods: *Pleurotomaria*? *pryceae* (J. de C. Sowerby), *Lophospira*? *angulata* (J. de C. Sowerby), *Holopella cancellata* (J. de C. Sowerby), *Phanerotrema* aff. *labrosum* (Hall), *Trochonema* sp., *Phanerotrema* sp., *Ruedemannia*? sp., *Raphistoma*? sp., *Cyclonema*? sp., platyceratid, holopaeacean, euomphalopterid. Bivalves: *Ctenodonta* sp., *Palaeoneilo* sp., *Actinodonta*? *hughesii* (Salter), *Cleionychia* sp. Cephalopod: *Phragmoceras pyriforme* (J. de C. Sowerby).

Wormwood Formation. Bellerophontid: *Bellerophon wenlockensis* (J. de C. Sowerby). Gastropods: turbiniform pleurotomariacean gen. nov., *Phanerotrema* sp., *Lophospira turrita* (Portlock), *Cyclonema tritorquatus* (M'Coy), holopaeacean. Cephalopods: *Cyrtoceras compressum* (J. de C. Sowerby), *Tretoceras*? *bisiphonatum* (J. de C. Sowerby).

Cerig Formation. Gastropod: *Planitrochus* sp.

Derwyddon Formation. Bellerophontid: *Kiaeromphalus* sp. Gastropods: *Gyronema* sp., *Phanerotrema*? sp. Cephalopods: *Actinoceras cochleatum* (Schlotheim), *Phragmoceras* sp.

It must be stressed that this is a provisional list; no substantial study of the molluscan fauna from the area has been made, although individual species have been described by J. de C. Sowerby *in* Murchison (1839), Blake (1882) and Reed (1920–21). In addition unidentified straight orthocone nautiloids are known from many localities in the area: Blake (1882) named four species.

(f) Other macrofossils

Both rugose and tabulate corals occur in the type Llandovery area and are abundant at some levels, but only very limited studies have yet been made of them. Dr D. Hill has identified the following from sectioned specimens. In addition we have collected a variety of specimens from many localities, but our field identifications are merely to genus group level.

Goleugoed Formation. *Streptelasma* cf. *araneum* (Smith), *S. crassiseptatum* Smith, *Plasmopora petalliformis* (Lonsdale).

Rhydings Formation. *Heliolites* cf. *parasiticus* Nicholson & Etheridge, *Calostylis* sp.

Wormwood Formation. *Favosites* sp., *Heliolites* sp., *Halysites* sp., *Pycnactis mitrata* (Schlotheim), *Calostylis* sp., *Phaulactis* sp., *Propora* cf. *magnifica* Počta.

Derwyddon Formation. *Halysites* sp., *Phaulactis* sp., *Lindstroemia* sp.

Bryozoans are also varied and abundant at many horizons but poorly studied, although Dr P. D. Taylor, BM(NH), has identified the commonest form in the Lower Llandovery as *Hallopora elegantula* (Hall).

Echinoderms are abundant in the form of crinoid ossicles; crinoid calyces are less common, but include glyptocrinids and cyclocrinids. Other groups occur sporadically, for example many specimens of the rhombiferan cystoid *Cheirocrinus* sp. were found in the Trefawr Formation at Loc. 151.

Receptaculitids and other sponges, hyolithids and also conulariids are all known as occasional specimens in the Goleugoed, Trefawr, Rhydings, Wormwood and Derwyddon Formations. Cricoconariids, informally identified as '*Tentaculites*' and '*Cornulites*', occur throughout the complete sequence.

(g) Microfossils

Acritarchs are abundant at most levels in the type Llandovery area and their distribution is described below (Appendix 1, p. 174); four main zones and a number of subzones can be recognized. Ostracods are rare in pre-Rhydings horizons, but can be abundant at some levels in the Upper Llandovery, although no work has been done on these from the type area. K. J. Dorning (personal communication) has collected chitinozoa and scolecodonts from the Goleugoed, Rhydings, Wormwood and Cerig Formations. They are present in moderate to low numbers in most palynological preparations, and are in general of moderate preservation. Outline investigations of the chitinozoa show they have some stratigraphical potential in the type Llandovery area. Conodonts are relatively scarce, but a limestone we collected from low in the Bronydd Formation (Loc. 92) was sent to R. J. Aldridge and I. Mohamed, who found in it the following conodonts: *Distomodus kentuckyensis* Branson & Branson, Pa, Pb, M and Sc elements; *Oulodus kentuckeyensis* (Branson & Branson), Pa and Sb elements; *Icriodella discreta* Pollock, Rexroad & Nicoll, Pa, Pb, M, Sb and Sc elements; and *Panderodus unicostatus* (Branson & Mehl), costate and simplexiform elements. This assemblage can be referred to the *Icriodella discreta–I. deflecta* Assemblage Zone in Britain, which spans a long interval from at or near the base of the Silurian to the early Upper Llandovery (Aldridge 1972).

Chronostratigraphy

(a) Stages within the Llandovery Series

In 1970, Cocks, Toghill and Ziegler proposed four stages, the Rhuddanian, Idwian, Fronian and Telychian, each with defined bases in the southern part of the type Llandovery area, apart from the base of the Rhuddanian which was defined at Dob's Linn, Scotland. There are two disadvantages of that classification. Firstly, the bases of the Idwian and Fronian (but not the Telychian) are in isolated outcrops, and secondly, it has been demonstrated by work subsequent to 1970 that the four stages are not of equal duration – the Idwian and Fronian appear shorter than the Rhuddanian and Telychian. The first disadvantage is in fact more theoretical than real, since the 'isolated' outcrops are parts of a simple stratigraphical sequence in the Ydw Valley which yields many fossils. However, it has been argued (and accepted by the Subcommision on Silurian Stratigraphy) that three stages for the Llandovery Series, rather than four, would make them of more comparable duration to those agreed for the Wenlock and Ludlow (although not for the Caradoc and Ashgill). Accordingly, we have taken advantage of our revision of the area to propose a three-stage system. The definitions of the stages are given below. The advantages of a new tripartite stage system are that the stages would be defined in continuously exposed fossiliferous sections, with a greater degree

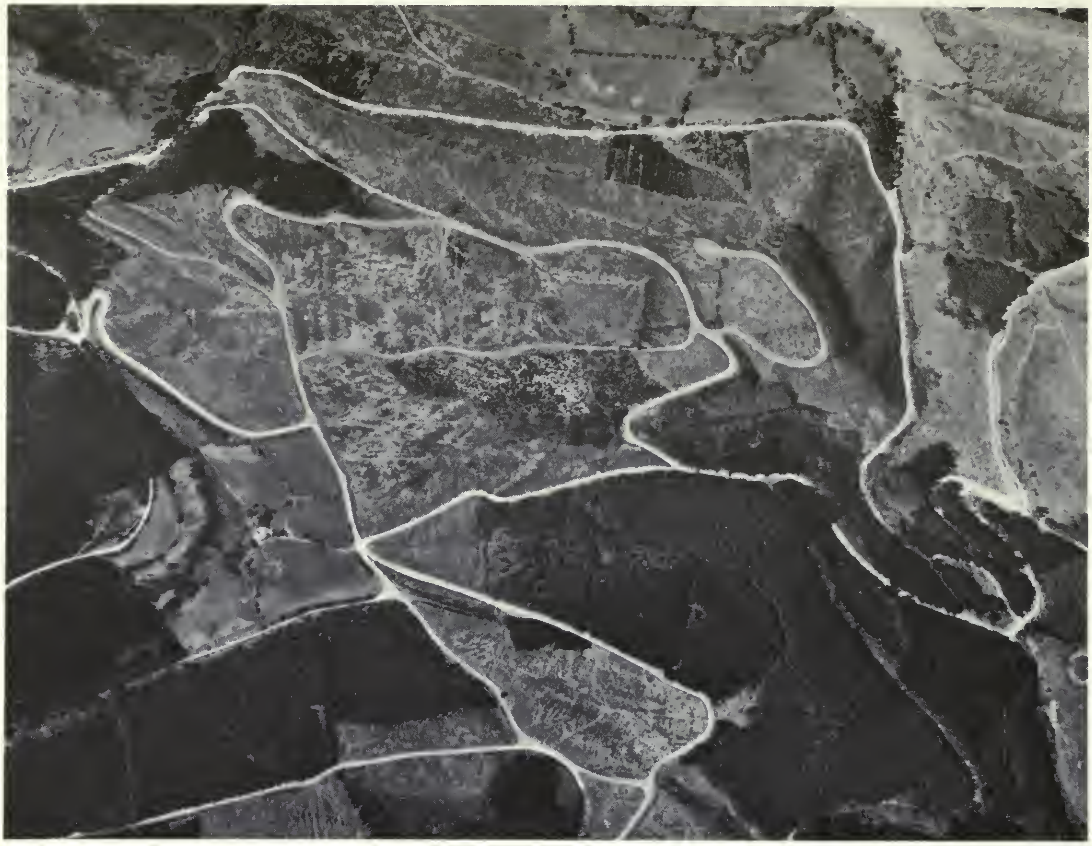

Fig. 59 Aerial photograph showing a few of the forestry tracks in the northern Llandovery area, including the Trefawr track area of Fig. 60 (reproduced by permission of the Director of Aerial Photography, Cambridge University). Approximate scale 1:10,000.

of detailed control than the previous scheme; the Llandovery Series would be subdivided more equally than hitherto; and the correlation between shelly and graptolitic facies would be even more accurate in view of our graptolite finds near the limits of our new stages. In addition, as discussed below in the section on international correlation, the two points taken as stage boundaries are capable of very wide correlation. We take the bases of the upper two stages in the tripartite stage system at the base of the *triangulatus* Zone (which is the same as the base of the broader *gregarius* Zone) and at approximately the base of the *turriculatus* Zone. The last horizon, although new as a stage boundary within the Llandovery Series, was particularly welcomed at the Podolian meeting of the Silurian Subcommission since both the *turriculatus* Zone and the underlying *sedgwickii* Zone are very widely recognized internationally; this is in contrast to a stage boundary at the base of the *sedgwickii* Zone, which is difficult to recognize when the underlying *convolutus* Zone is not developed, as is the case in many places.

It should be noted that the new scheme disrupts the usage, unambiguous since the work of Murchison, of the term 'Upper Llandovery', although Murchison's 'Lower Llandovery' had already been redefined into a new 'Lower' and 'Middle' Llandovery by Jones (1925). Our new stage boundaries, although dividing Llandovery time more nearly equally into three parts, do not coincide with the Lower, Middle and Upper divisions of Jones.

However, one of us (JTT) dissents from the conclusions in this section of the report and considers that the most natural subdivision of the Llandovery Series, both at Llandovery and

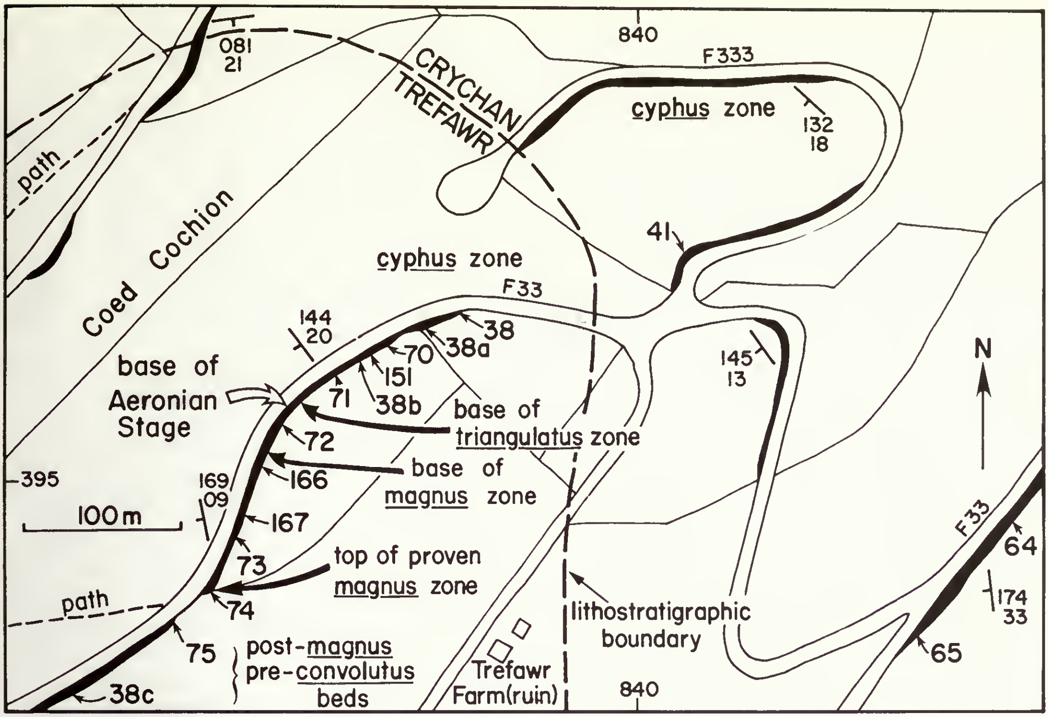
081
21
CRYCHAN
TREFAWR
840
F333
cyphus zone
132
18
path
Coed Cochion
41
cyphus zone
F33
144
20
38
70
38a
151
71
38b
base of Aeronian Stage
base of triangulatus zone
72
166
base of magnus zone
395
169
09
100m
167
73
top of proven magnus zone
path
74
75
post-magnus pre-convolutus beds
38c
Trefawr Farm(ruin)
lithostratigraphic boundary
840
145
13
N
F33
64
174
33
65

Fig. 60 Map of the base of the Aeronian Stage on the F 33 Trefawr track (transect h of Figs 3 and 4). Rock outcrops are shown in dense black: the larger numbers are our localities; the smaller numbers dips and strikes. Forestry Commission track numbers are preceded by F.

elsewhere, is into two stages, which can be widely recognized on both shelly and graptolitic faunas. In the Llandovery area a convenient base for an upper stage would be at Loc. 89 (transect h) on the Trefawr track, grid reference SN 8343 3923, which coincides approximately with the base of Jones' (1925) original C_1 division of the Upper Llandovery, and is mappable over most of the area. The basal beds of the upper stage yield *sedgwickii* Zone graptolites, a zone which is widely known internationally, and two important brachiopods characteristic of the higher part of the Llandovery (*Pentamerus oblongus* and *Eocoelia*) appear for the first time near to the base of the upper stage in the type area.

(b) The Rhuddanian Stage

The lowest stage may still be termed the Rhuddanian, but it is not considered fully here since its base is defined to be coincident with the Ordovician–Silurian boundary at the base of the *acuminatus* Zone at Dob's Linn, Scotland, rather than at the base of the *persculptus* Zone as originally defined by Cocks *et al.* (1970). The exact correlation of that horizon is not known in the type Llandovery area, but it is above the *Hirnantia*-bearing beds of the Scrach Formation and must be at or near the base of the Bronydd Formation. Its top is still at the same horizon as originally proposed, and there are many good developments of rocks and fossils representing the stage in the type Llandovery area, in particular the forestry track section near Scrach (transect i).

(c) The Aeronian Stage

We propose the new name Aeronian for this middle stage, named after Cwm-coed-Aeron Farm, 500 m south of the type section of the Trefawr track. Its base is defined at the base of the *triangulatus* Zone and the top is defined by the base of the revised Telychian Stage (see below). We considered two alternative bases to the Aeronian Stage, the base of the

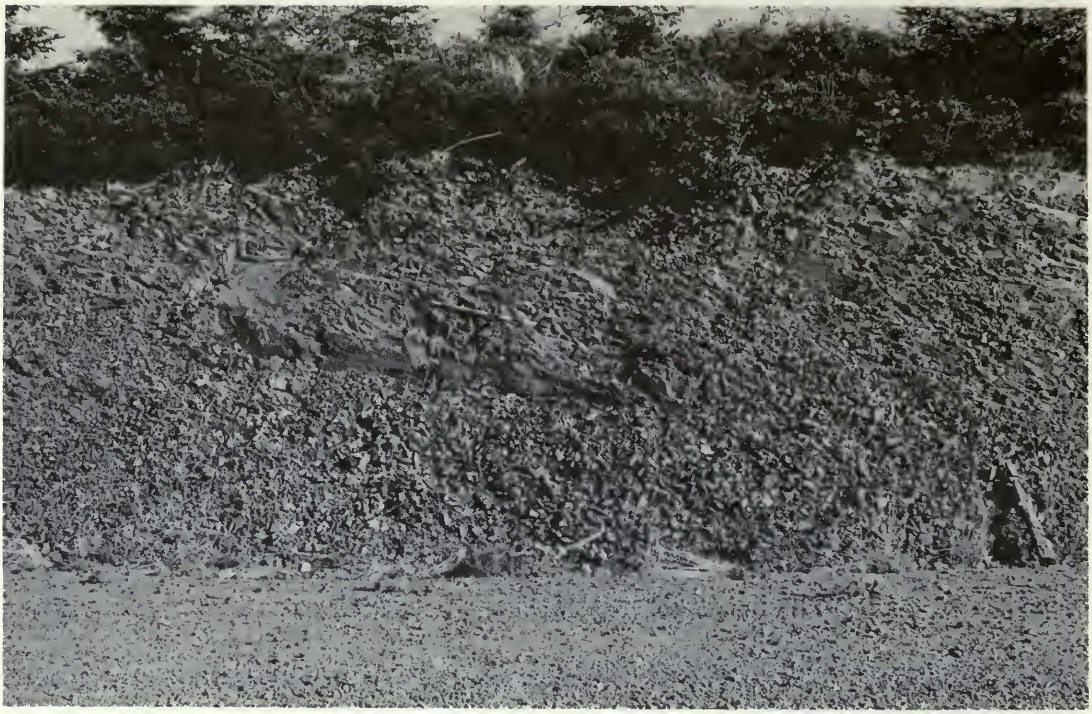

Fig. 61 Stratotype base of the Aeronian Stage, Trefawr track, base of Loc. 72, Grid Reference SN 8380 3953, northern Llandovery area. The Trefawr track has continuous rock exposures for several hundred metres either side of this locality (see Figs 59 and 60).

triangulatus Zone as seen in transect h at the base of Loc. 72 (g.r. SN 8380 3953), or the base of the *magnus* Zone in the same section, the Trefawr track (Fig. 60) at the base of Loc. 166 (SN 8378 3950). The *magnus* fauna is the more widely recognizable within the Llandovery district itself, although the *triangulatus* Zone is recognized on three major sections, namely those of transects d, f and h. Both are recognized in the north and in the south of the type area, their bases being respectively within the Trefawr Formation and the Coldbrook Formation. However, the base of the *triangulatus* Zone has much the greater potential for international correlation either as the zone of this name or as the base of the broader *gregarius* Zone. Both depend upon the first appearance of triangulate monograptid species and the genera *Rastrites* and *Petalograptus*, and their bases are effectively coincident. The faunas have been identified on a more or less world-wide basis. For this reason we prefer to take the base of the Aeronian Stage at the base of the *triangulatus* Zone.

We define the base of the stage in a gently dipping section of blocky mudstones within the Trefawr Formation (Figs 61 and 62). The fauna is common, but dispersed throughout the rock and is only occasionally concentrated into shelly bands. Near the boundary the fauna consists chiefly of shelly fossils, mainly brachiopods (Fig. 63), but bivalves, gastropods, cephalopods, trilobites, rugose and tabulate corals, bryozoa, cystoids, tentaculitids and other phyla all occur in the macrofauna. Graptolites are also present at every horizon sampled, and the more important species are also shown in Fig. 63. The stage boundary is defined at the base of the *triangulatus* Zone, which is represented in the Trefawr section by the incoming of *Monograptus austerus sequens* Hutt. That this is effectively the base of the *triangulatus* Zone is demonstrated by the occurrence of *Monograptus austerus vulgaris*, the *cyphus* Zone ancestor of *sequens*, in the Trefawr section below at Loc. 70. The top of the *cyphus* Zone is also confirmed by the record of *Diplograptus elongatus* Churkin & Carter, which has never been recorded from above that zone.

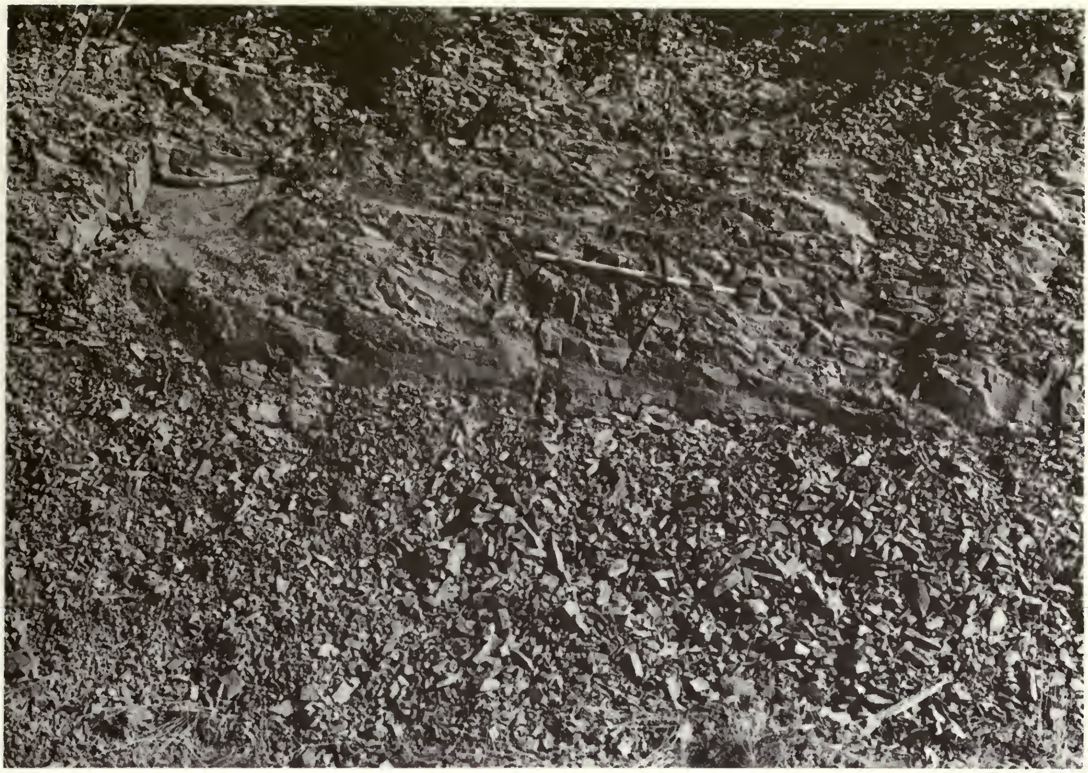

Fig. 62 Stratotype base of the Aeronian Stage, enlarged detail of Fig. 61. The metre rule is parallel with the dip of the blocky mudstones. The actual base is at the base of the centimetre rule to the left of the metre rule.

On the neighbouring transect f, Loc. 100, at the same stratigraphical level as Loc. 72, yields *Monograptus* cf. *revolutus* Kurck, *s.s.*, *Monograptus triangulatus* ? *separatus* Sudbury, *Monograptus triangulatus* ?*fimbriatus* (Nicholson), *Rhaphidograptus toernquisti* (Elles & Wood) and *Diplograptus* sp., which together also indicate the *triangulatus* Zone.

(d) The Telychian Stage

The highest stage will still be termed the Telychian, although its base is revised upwards from the base of the Wormwood Formation (Cocks *et al.* 1970: 83), the old C_4 division of Jones (1925), up to near the top of the Wormwood Formation, which allows much better international correlation. From our recent collecting we are able to confirm Ziegler's (1966) records of the rhynchonellid *Eocoelia intermedia* (Hall) in the upper part of the Rhydings and all through the Wormwood Formation, including Locs 162 and 162 on the Cefn Cerig Road section (Fig. 6, transect d). In the lowest parts of the overlying Cerig Formation (e.g. at Loc. 163) the earliest forms of the succeeding species *Eocoelia curtisi* are present, including specimens in which the umbonal chambers of *intermedia* and earlier forms are present only as relicts fused to the hinge line, indicating the point of transition between the two species, and we define the base of the Telychian at just above the highest record of true *intermedia*. This level is much more exactly correlatable than the previously defined base of the Telychian (Loc. 158 in the same Cefn Cerig Road section – Fig. 64).

The new base of the Telychian is defined in a quarry immediately west of the Cefn Cerig Road (Figs 64–66) at Grid Reference SN 7743 3232. The lithology consists of a series of siltstones with occasional sandy siltstones and muddy siltstones within the Wormwood Formation, which represents normal open shelf marine deposition without turbidites, with most of the beds bioturbated. Some shells occur in almost every bed, but a particularly

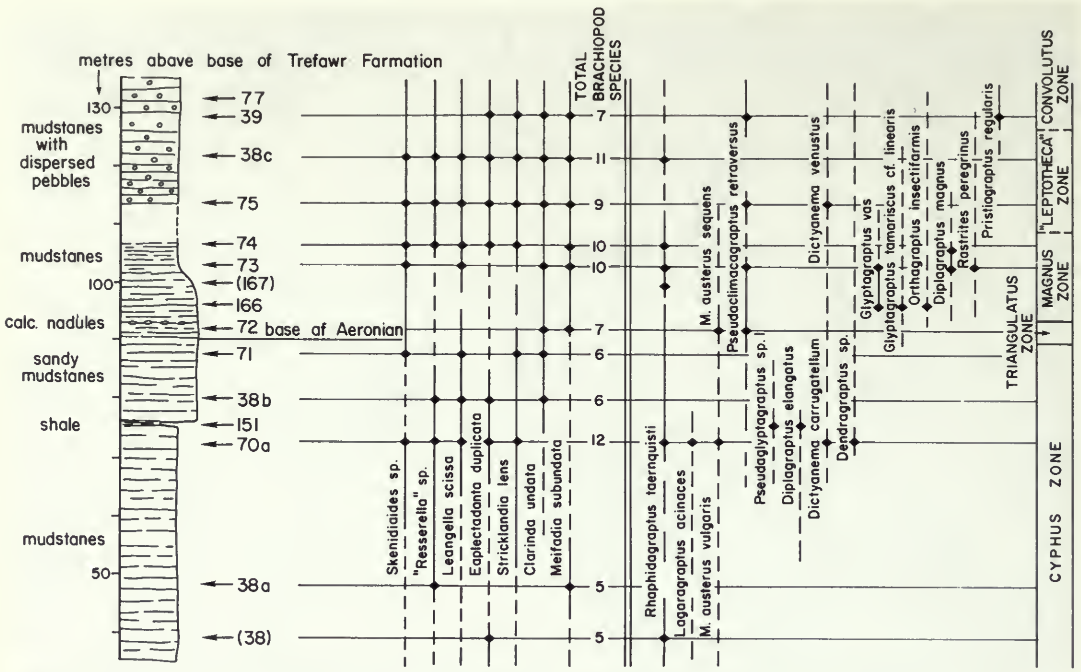

Fig. 63 Fauna of brachiopods and graptolites at selected intervals across the Rhuddanian–Aeronian boundary in the Trefawr track section. The locality numbers are shown on the left.

fossiliferous horizon (Loc. 162) just below the boundary (Fig. 67) yields 25 different species of macrofauna, many in abundance, and includes the highest records of the brachiopods *Eocoelia intermedia* (Hall) and *Stricklandia lens progressa* Williams, both widely recognized in international correlation (Ziegler 1966, Williams 1951 etc.). The succeeding species *Eocoelia curtisi* Ziegler and *Stricklandia laevis* (M'Coy) are both known from the overlying Loc. 163, and the stage boundary is defined here just above the last occurrence of *E. intermedia* at Loc. 162.

This horizon is widely recognizable and (at the limits of present stratigraphical precision) coincides with the base of the *turriculatus* graptolite zone; for a recent map of its distribution in Europe and eastern North America see Cocks & Fortey 1982: 473. Graptolites are not known from near the basal boundary of the Telychian in the Cefn Cerig Road section, but we have found a graptolite fauna referable to the *turriculatus* Zone at two localities in the Cerig Formation, one near the base of the formation at Loc. 131, transect n, yielding *Monograptus runcinatus* Tullberg: this graptolite is known world-wide and only from the lower half of the *turriculatus* Zone in the best documented sections. *Sedgwickii* Zone graptolites are known from a horizon over 400 m stratigraphically below the base of the revised Telychian. Thus the Aeronian–Telychian boundary probably correlates approximately with the lower boundary of the *turriculatus* Zone: this is confirmed by the distribution of the relevant *Eocoelia* species and graptolites in Penwhapple Glen, Girvan (Cocks & Toghill 1973). This horizon also correlates with the base of the Zone 4 acritarch fauna of Hill (1974 and see Appendix 1, p. 175), characterized by the incoming of *Deunffia monospinosa* Downie, *Domasia bispinosa* Downie and *Pterospermella* cf. *foveolata* Lister *in* Dorning (1981).

The basal Telychian Stage boundary is also to be found in the Glyn moch section (Fig. 4, transect f) at g.r. SN 8179 3755, which forms part of a continuously exposed section of over 400 m stratigraphical thickness in a Forestry Commission track. There, shells are common up

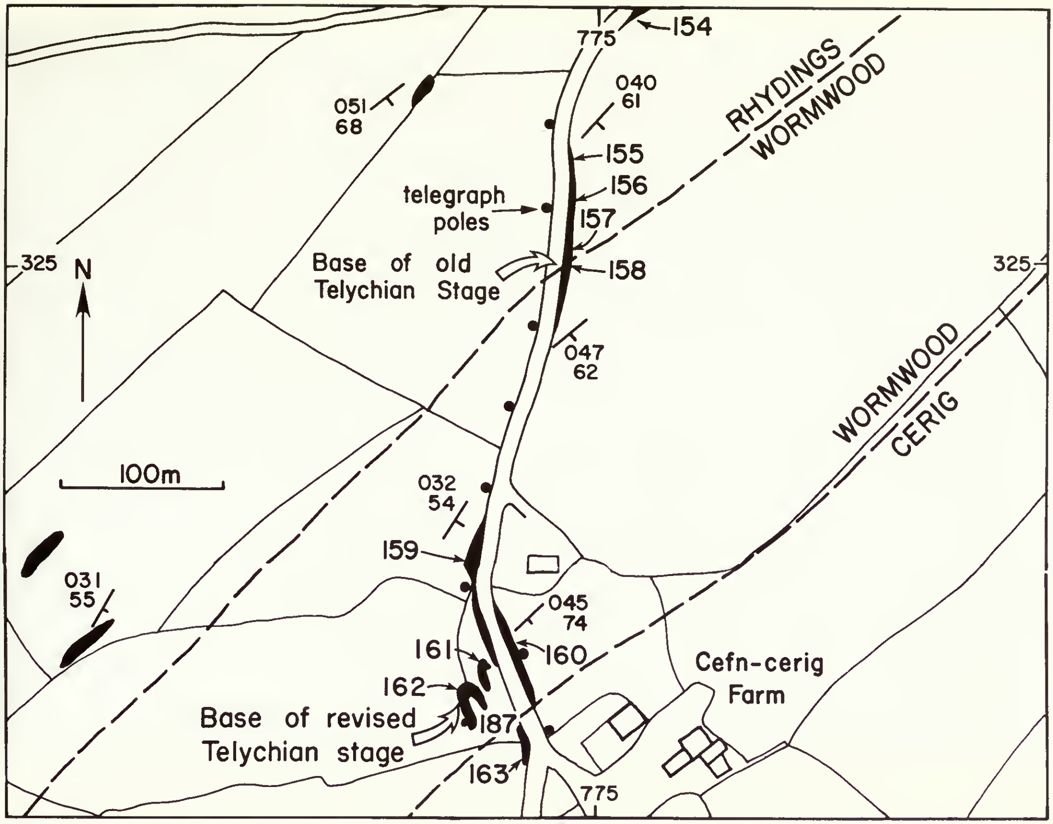
775
154
051
68
040
61
RHYDINGS
WORMWOOD
155
156
telegraph poles
157
Base of old Telychian Stage
158
325
N
325
047
62
WORMWOOD
CERIG
100m
032
54
159
031
55
045
74
161
160
162
Cefn-cerig Farm
Base of revised Telychian stage
187
163
775

Fig. 64 Map of the base of the revised Telychian Stage on the Cefn Cerig road section (transect d of Figs 2 and 4).

to the top of the Wormwood Formation (Locs 5, 6), though sparser in the basal part of the Cerig Formation, but the overlying Loc. 140, 7m above the base of the Cerig Formation, carries a *turriculatus* Zone graptolite fauna. Although *Stricklandia* occurs in this section, the critical species of *Eocoelia* have not yet been found there.

International correlation

(a) Graptolites

It is probable that a complete sequence of graptolite zones exists in the type Llandovery area from the latest Ordovician to the *turriculatus* Zone of the upper Llandovery. Above this level graptolite zones are likely to be identified only on chance and rare finds. Below the *turriculatus* Zone graptolites are not uncommon, and provide relatively rich faunas in the Trefawr Formation. It has been possible to establish positively the presence of the *cyphus, triangulatus, magnus, convolutus, sedgwickii* and *turriculatus* Zones, probably the *acuminatus* level (though without rich faunas) and graptolitic strata almost certainly equivalent to the *persculptus, atavus, acinaces* and *leptotheca* Zones but which have yet to yield definitive species in association with the more common and longer-ranging graptolites. All these zones can be correlated on an international basis. Indeed several new records for the United Kingdom reinforce an already strong correlative framework, and include *P.* (*M.*) *fidus* (or *pictus*) Koren' & Mikhailova and *D.* aff. *elongatus* Churkin & Carter. Figs 7, 19 and 68

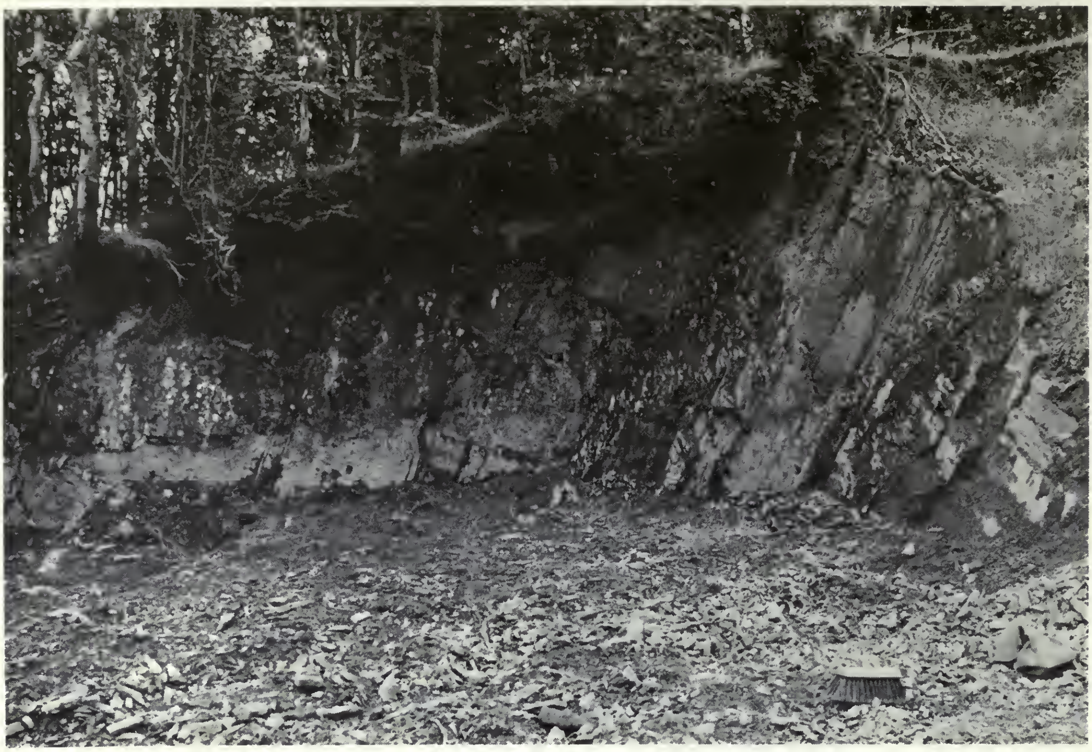

Fig. 65 Stratotype base of the Telychian Stage, Loc. 162, Wormwood Formation, old quarry west of Cefn Cerig road, Grid Reference SN 7743 3232, southern Llandovery area. The exposure continues for 9 m to the left and 17 m to the right of the photograph, and is part of the Cefn Cerig road section (see Fig. 64).

summarize the occurrence of graptolites against the lithostratigraphic and suggested biostratigraphic sequences.

(b) Shelly fossils

International correlation of rocks of Llandovery age has been effected by many authors by the study of evolving lineages of brachiopods. Chief of these is *Stricklandia* (Williams 1951, Amsden 1966, Rubel' 1977, Johnson 1979, Baarli & Johnson 1982), whose species and subspecies have been widely identified in Europe, the U.S.S.R., North America and elsewhere. All of the subspecies recognized by Williams (1951) were originally described from the type Llandovery area, and all of the successive constituents of the lineage are known from there, apart from the highest (*Costistricklandia lirata*). However, despite the work of Baarli and Johnson (1982) who measured successive samples of early Llandovery *Stricklandia* from the Oslo region, Norway, and who were able to separate *S. lens prima* from *S. lens lens* on measurements of their cardinalia, we are not able to confirm the separation of early Llandovery *Stricklandia* subspecies in our work, and merely show the stratigraphical position of Williams' type specimens of *S. lens prima, S. lens lens* and *S. lens intermedia* on our Fig. 69. In the upper part of the Llandovery successions, the evolution of *Eocoelia* (Ziegler 1966) has also been useful, and three successive species, *hemisphaerica, intermedia* and *curtisi* are recorded from Llandovery. Pentamerinids, atrypids and some stropheodontaceans have also been used, and these are all known from the type Llandovery area. Thus the Llandovery type area can be correlated accurately with the many other Llandovery age rocks containing shelly fossils, both elsewhere in Britain and in key areas

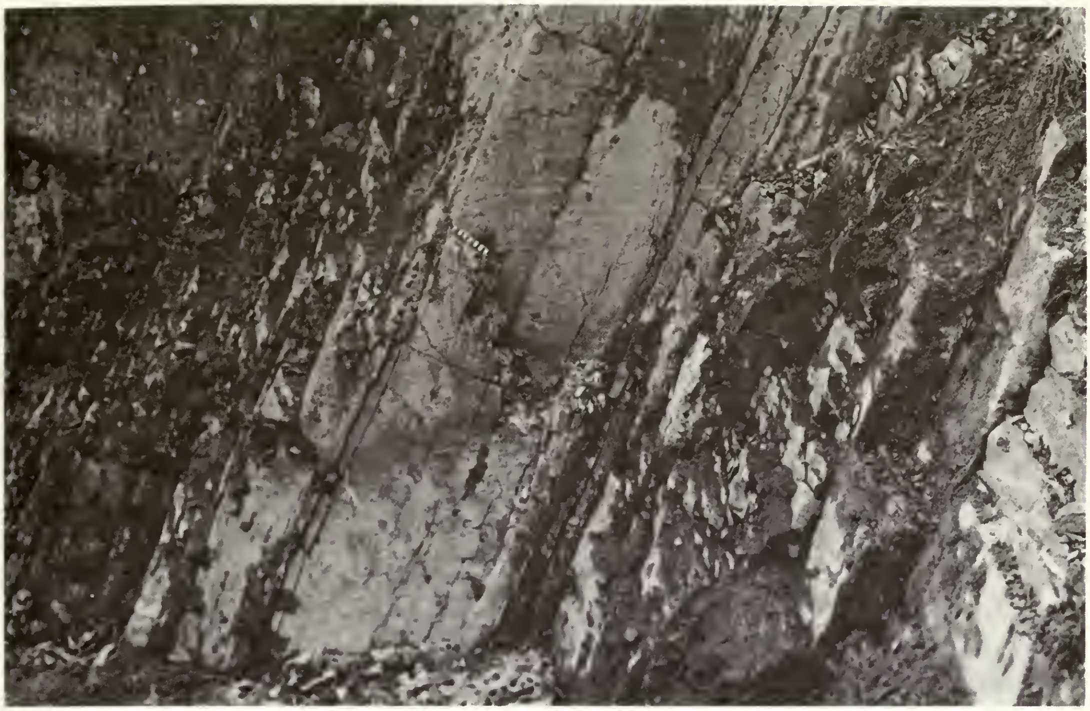

Fig. 66 Stratotype base of the revised Telychian Stage, enlarged detail of Fig. 65. The base is at the right hand end of the centimetre rule, within a 29 cm thick bioturbated shelf siltstone bed. The section youngs to the left of the photograph (the south).

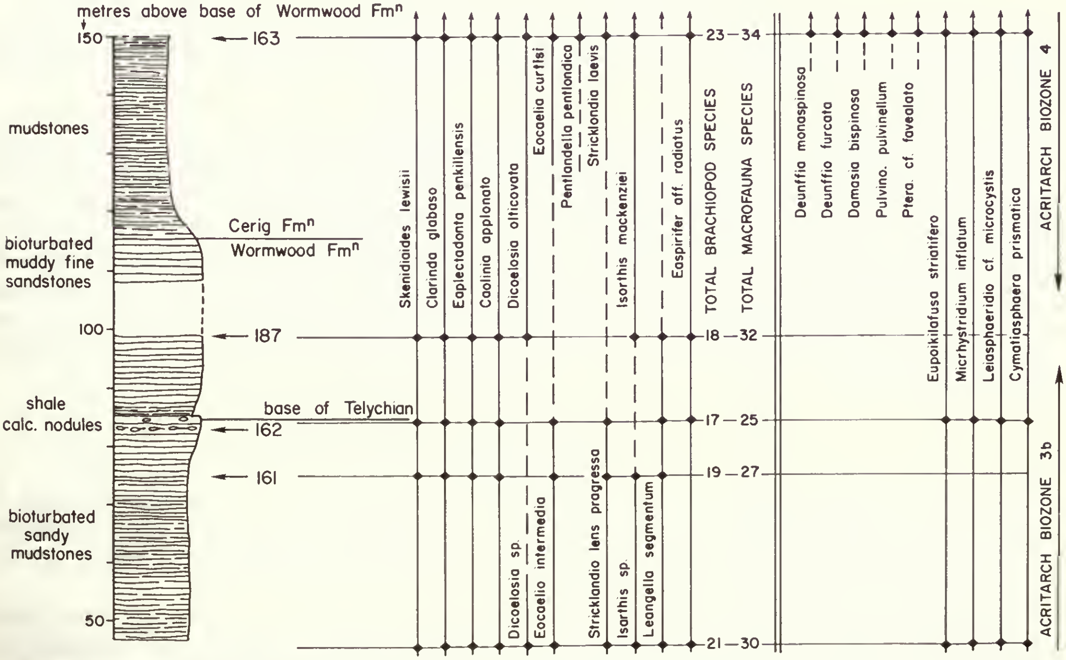

Fig. 67 Selected brachiopod and acritarch species across the Aeronian–Telychian stage boundary in the Cefn Cerig road section (transect d of Figs 2 and 4).

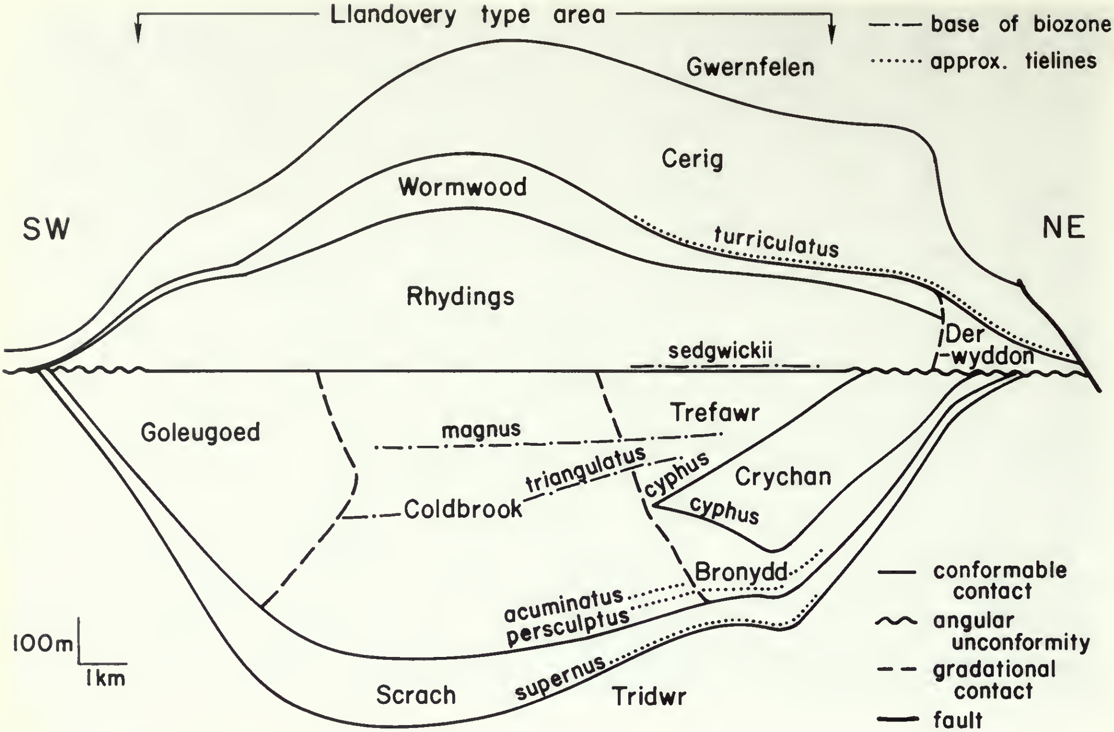
Llandovery type area
—·— base of biozone
······· approx. tielines
Gwernfelen
Cerig
Wormwood
SW
NE
turriculatus
Rhydings
Der-wyddon
sedgwickii
Trefawr
Goleugoed
magnus
triangulatus
cyphus
Crychan
Coldbrook
cyphus
Bronydd
acuminatus
persculptus
supernus
Scrach
Tridwr
100m
1km
— conformable contact
angular unconformity
– – gradational contact
— fault

Fig. 68 Graptolite zones in relation to lithostratigraphy in the type Llandovery area.

abroad, including the Oslo region, Norway (Worsley 1982), and Anticosti Island, Canada (Barnes & McCracken 1981).

(c) Microfossils

No microfossil group is as yet very refined for the international correlation of rocks of Lower Silurian age. Only four conodont zones and four acritarch zones are established for the entire span of Llandovery time (by contrast to the 14 or more graptolite zones established for the same interval). Acritarchs are abundant in the type Llandovery area (see Appendix 1, p. 174), and reveal all the known zones (Hill 1974a); however, conodonts are relatively scarce, although the *Icriodella discreta–I. deflecta* Assemblage Zone is now known from our work in the Bronydd Formation. Chitinozoa and ostracods both occur in the type Llandovery area, but effective zonations have not yet been established for these groups in Britain or elsewhere.

Conclusions

1. Our new mapping has revealed that the development of rocks of Llandovery age is complete in the Llandovery type area: there is a continuous sequence from Ashgill through Llandovery to Wenlock age, with no detectable unconformities (except at the lateral flanks of the basin).
2. With the recent cutting of forestry tracks to add to the previous outcrops, there are long reaches of continuous exposure, providing adequate primary and confirmatory sections for collecting and research. Permanent access to the area and protection of the sections can be guaranteed through the Nature Conservancy.

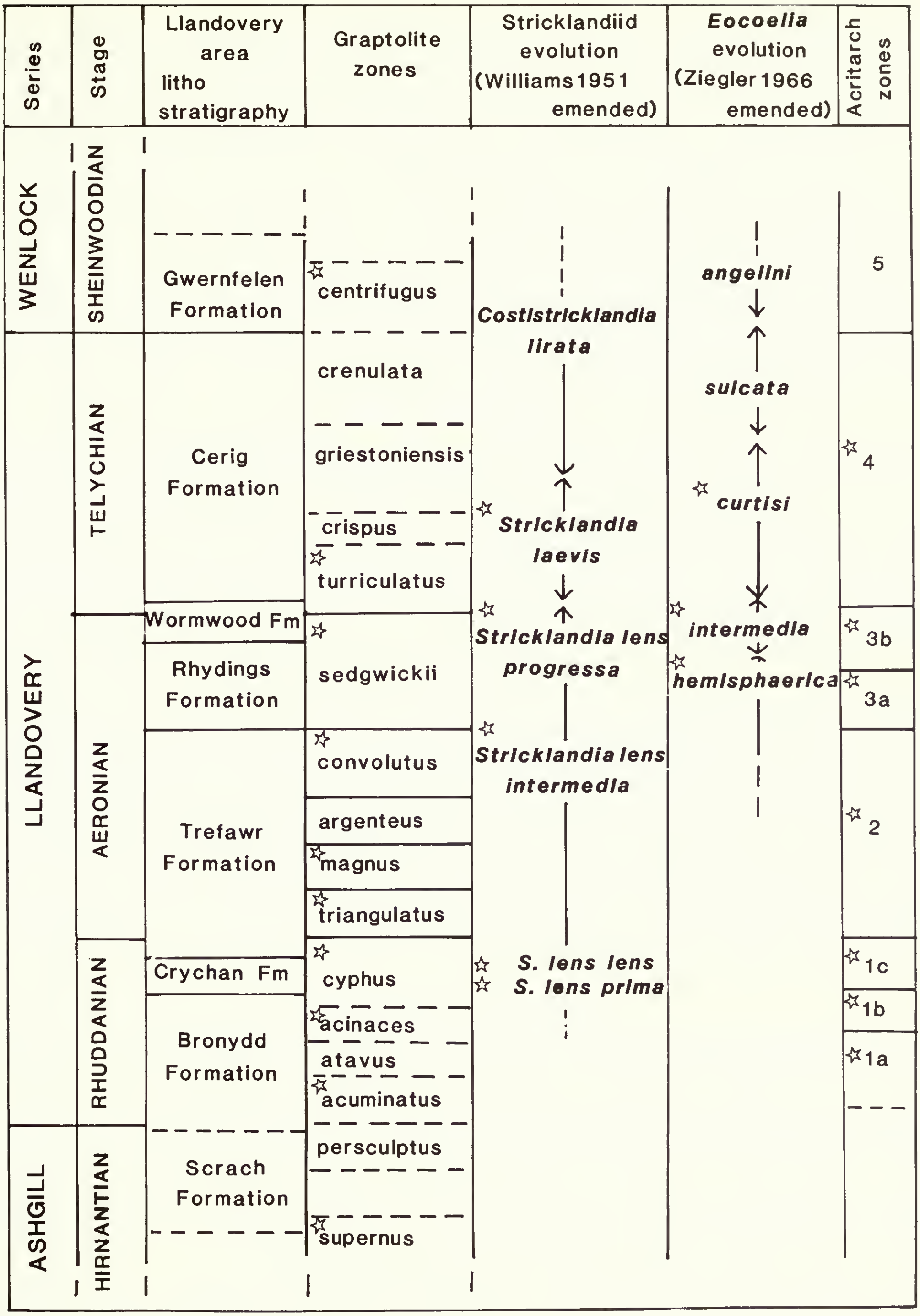
Series
Stage
Llandovery area litho stratigraphy
Graptolite zones
Stricklandiid evolution (Williams 1951 emended)
Eocoelia evolution (Ziegler 1966 emended)
Acritarch zones
WENLOCK
LLANDOVERY
ASHGILL
SHEINWOODIAN
TELYCHIAN
AERONIAN
RHUDDANIAN
HIRNANTIAN
Gwernfelen Formation
Cerig Formation
Wormwood Fm
Rhydings Formation
Trefawr Formation
Crychan Fm
Bronydd Formation
Scrach Formation
☆ centrifugus
crenulata
griestoniensis
crispus
☆ turriculatus
☆ sedgwickii
☆ convolutus
argenteus
☆ magnus
☆ triangulatus
☆ cyphus
☆ acinaces
atavus
☆ acuminatus
persculptus
☆ supernus
Costistricklandia lirata
☆ Stricklandia laevis
☆ Stricklandia lens progressa
☆ Stricklandia lens intermedia
☆ S. lens lens
☆ S. lens prima
angelini
sulcata
☆ curtisi
☆ intermedia
☆ hemisphaerica
5
☆ 4
☆ 3b
☆ 3a
☆ 2
☆ 1c
☆ 1b
☆ 1a

Fig. 69 Correlation of the Llandovery Series, showing our new lithostratigraphy and stage divisions, the standard scale of graptolite zones, the evolution of the brachiopods *Stricklandia* and *Eocoelia* and the acritarch zones of Hill (Appendix 1, p. 175). Zones and fossils with ☆ are known from the type Llandovery area.

3. The brachiopod faunas, including the important stricklandiids, pentameridines, *Eocoelia* and others, are abundant at numerous significant levels: to these we can now add the newly-discovered *Hirnantia* fauna from immediately beneath the type Llandovery. Trilobites, molluscs, echinoderms, corals, bryozoa and other shelly faunas also occur.
4. It is probable that a complete sequence of graptolite zones exists in the type Llandovery area from the latest Ordovician to the *turriculatus* Zone of the late Llandovery.
5. Substantial numbers of acritarchs from all levels have been demonstrated, including all the established zones, and some conodont faunas are also present, although only the *Icriodella discreta–I. deflecta* Assemblage Zone is yet confirmed.
6. The Llandovery area has been the international standard for rocks of Lower Silurian age since 1857. The good exposure and comprehensive faunas, both shelly and graptolitic, enables us to be in a position to define a three-stage division of the Llandovery Series in the type area, namely the Rhuddanian, Aeronian and Telychian, and the bases of the upper two stages are described in detail here.

Acknowledgements

We are most grateful to Amanda Chapman and Dr K. M. Evans for assistance in field work and laboratory, and to members of the Ludlow Research Group for other finds. Professor C. H. Holland and Dr M. G. Bassett also accompanied us on our initial field work. Dr M. A. Woollands generously made his unpublished thesis and maps available to us and Drs R. J. Aldridge, N. J. Morris, A. B. Smith and P. D. Taylor helpfully identified some of our collections. We also thank the Forestry Commission, through Mr I. Watt, who facilitated access to part of the area, and the Nature Conservancy Council, through Dr W. A. Wimbledon, who kindly arranged for the clearance of some localities.

Note

Following the circulation of a preliminary cyclostyled version of this paper, the Subcommission on Silurian Stratigraphy voted early in 1984 on the proposals suggested in this paper and on other matters, and in a Subcommission circular dated July 1984 it was announced that the Titular Members had voted in favour of the name Llandovery for the earliest series of the Silurian (by 14 votes to 1), and in favour of a three-stage system based on the type Llandovery area, namely the Rhuddanian, Aeronian and Telychian Stages as defined in the present paper (by 10 votes to 3, with 2 abstentions). These decisions were forwarded to the International Commission on Stratigraphy of the International Union of Geological Sciences for ratification.

Appendix 1. Acritarchs

by P. J. Hill (Division of Geology, Derby College of Higher Education, Kedleston Road, Derby DE3 1GB) & K. J. Dorning (Pallab Research, 58 Robertson Road, Sheffield S6 5DX).

Acritarchs have been recorded from all formations in the type Llandovery area. They are common to abundant in all samples apart from the sandstone facies of the Scrach Formation, where they are rare or absent. Preservation is variable, mostly good to moderate, occasionally poor. The moderate organic thermal maturation, indicated by the medium to dark brown coloration of the simple-walled acritarchs, is unlikely to have significantly affected the acritarch preservation.

62 different acritarch species have been recorded from the Llandovery area, as follows.

Ammonidium microcladum (Downie) Lister 1970, *A.* sp. 1 of Hill 1974 (numerous very short processes), *Baltisphaeridium archaicum* Cramer & Díez 1972, *Carminella maplewoodensis* Cramer 1968, *Cymatiosphaera prismatica* Deunff 1954, *Dactylofusa estillis* Cramer & Díez 1972, *Deunffia monospinosa* Downie 1960, *Dictyotidium dictyotum* (Eisenack) Eisenack 1955, *D. stenodictyum* Eisenack 1965, *Diexallophasis denticulata* (Stockmans & Willière) Loeblich 1970, *D. granulatispinosa* (Downie) Hill 1974, *Dilatisphaera dameryensis* Dorning 1981, *D. williereae* (Martin) Lister 1970, *Domasia trispinosa* Downie 1960, *D. bispinosa* Downie 1960, *D. limaciforme* (Stockmans & Willière) Cramer 1970, *Duvernaysphaera aranaides* Cramer 1964, *Electoriskos pogonius* Loeblich 1970, *Estiastra magna* Eisenack 1959, *Eupoikilofusa striatifera* (Cramer) Cramer 1970, *Helosphaeridium citrinipeltatum* (Cramer) Dorning 1981, *Leiofusa banderillae* Cramer 1964, *L. parvitatis* Loeblich 1970, *L.* cf. *tumida* Downie 1959, *Leiosphaeridia laevigata* Stockmans & Willière 1963, *L.* cf. *microcystis* (Eisenack) Downie 1959, *L. wenlockia* Downie 1959, *Lophosphaeridium* cf. *granulosum* (Staplin) Downie 1963, *L. parverarum* Stockmans & Willière 1963, *Metaleiofusa* sp. 1 (small elongate vesicle), *M.* sp. 2 (inflated vesicle), *M.* sp. 3 (very elongate vesicle), *Micrhystridium inflatum* (Downie) Lister 1970, *M. nanum* Deflandre 1945, *M. nannacanthum* Deflandre 1945, *M. parinconspicuum* Deflandre 1945, *M.* cf. *parinconspicuum, M. parveroquesi* Stockmans & Willière 1963, formgroup *M. stellatum* Deflandre 1945, *M.* cf. *vulgare* Stockmans & Willière 1962, *Multiplicisphaeridium arbusculum* Dorning 1981, *M. fisherii* (Cramer) Lister 1970, *M. imitatum* (Deflandre) Lister 1970, *M. micropilaris* (Cramer) Eisenack & Cramer 1973, *M. paraguaferum* (Cramer) Lister 1970, *M. rochesterensis* Cramer & Díez 1972, *Oppilatala* cf. *eoplanktonica* (Eisenack) Dorning 1981, *O. ramusculosa* (Deflandre) Dorning 1981, *Pterospermella* cf. *foveolata* Lister *in* Dorning 1981, *Pulvinosphaeridium pulvinellum* Eisenack 1954, *Salopidium granuliferum* (Downie) Dorning 1981, formgroup *Tunisphaeridium parvum* Deunff & Evitt 1968, *T. tentaculiferum* (Martin) Cramer 1970, *Tylotopalla robustispinosa* (Downie) Eisenack & Cramer 1973, *Veryhachium formosum* Stockmans & Willière 1960, *V. lairdii* (Deflandre) Deunff *ex* Downie 1959, *V. rhomboidium* Downie 1959, *V. scabratum* Cramer 1964, formgroup *V. trispinosum* (Eisenack) Cramer 1964, *V. valiente* Cramer 1964, *V. wenlockium* Downie 1959, *Visbysphaera meson* (Eisenack) Lister 1970.

Fifteen of the above species are long-ranging, and have been recorded in samples throughout most of the Rhuddanian, Aeronian and Telychian: *Ammonidium* sp. 1, *Diexallophasis denticulata, Leiofusa* cf. *tumida, Leiosphaeridia wenlockia, Lophosphaeridium* cf. *granulosum, L. parverarum, Metaleiofusa* sp. 2, *Micrhystridium nanum, M. parinconspicuum*, formgroup *M. stellatum, Oppilatala ramusculosa, Veryhachium rhomboidium*, formgroup *V. trispinosum*, and *V. wenlockium.*

Fig. 70 lists 45 species of restricted stratigraphical range in the southern Llandovery area. None of these are known from the Ashgill of the Llandovery area, while 14 are known to extend into the Wenlock in the Llandovery area. Additional data from the central and northern Llandovery areas, and other localities within the Welsh Basin, have shown many of the species to be similarly stratigraphically restricted. On the basis of all these data, seven acritarch assemblage biozones can be recognized in the Llandovery area, as follows.

Biozone 1a. Base of range of *Helosphaeridium citrinipeltatum. Baltisphaeridium archaicum* appears to be restricted to this zone. *Diexallophasis granulatispinosa, Dictyotidium dictyotum* and *Micrhystridium* cf. *parinconspicuum* have a base of range within this zone.

Biozone 1b. Base of range of *Metaleiofusa* sp. 1 and *Tylotopalla robustispinosa. Micrhystridium* cf. *parinconspicuum* is common.

Biozone 1c. Base of range of *Micrhystridium* cf. *vulgare* and *M. parveroquesi. Micrhystridium* cf. *parinconspicuum, Multiplicisphaeridium fisherii* and *Multiplicisphaeridium rochesterensis* are often recorded.

Biozone 2. Base of range of *Multiplicisphaeridium paraquaferum* and *Oppilatala* cf. *eoplanktonica. Tunisphaeridium tentaculiferum, Leiofusa banderillae* and *Domasia trispinosa* first occur within this zone. The base of biozone 2 is at about the base of the Rhydings Formation.

Biozone 3a. Base of range of *Domasia limaciforme, Metaleiofusa* sp. 3 and *Ammonidium microcladum. Leiofusa parvitatis, Multiplicisphaeridium arbusculum* and *Salopidium granuliferum* appear for the first time within this zone.

Biozone 3b. Base and top of range of *Dactylofusa estillis. Dilatisphaera williereae, Domasia limaciforme, Multiplicisphaeridium fisherii* and *Tunisphaeridium tentaculiferum* are frequently recorded.

Biozone 4. Base of range of *Deunffia monospinosa, D. furcata, Domasia bispinosa.* The base of biozone 4 approximates to the base of the Cerig Formation, the base of the redefined Telychian.

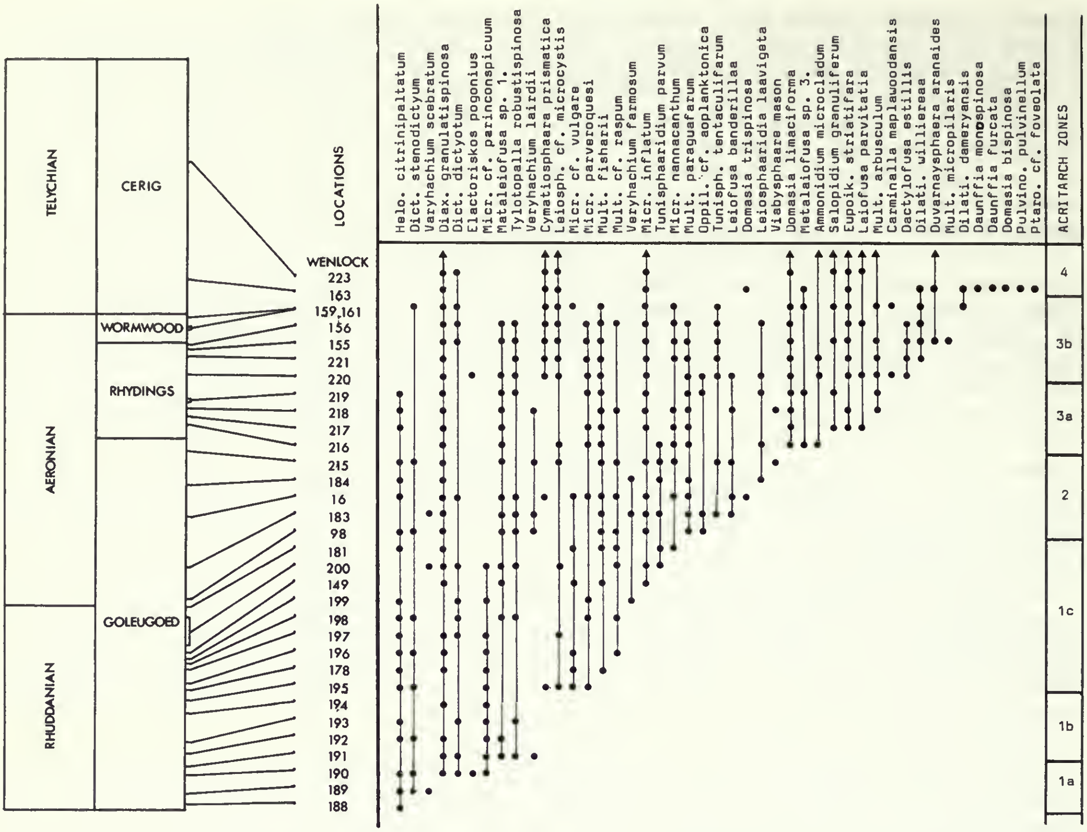

Fig. 70 Ranges of selected acritarch species in the type Llandovery area, chosen from the 62 species recorded, to illustrate the acritarch zones recognized (by P. J. Hill & K. J. Dorning).

The acritarch biozones recorded from the type Llandovery area can be recognized at many localities in Wales and the Welsh Borderland. Acritarchs characteristic of all the zones have been recognized from many localities in north-west Europe and eastern North America. However, acritarchs characteristic of the acritarch biozone W1 (Dorning 1981, = Zone 5 of Hill, 1974) which has a base 150 mm below the base of the type Wenlock at Leasows in Shropshire have not been recorded from the Cerig Formation.

Recycled acritarchs, dominated by forms of Tremadoc age, are present in many Rhuddanian and Aeronian samples. Of the total acritarchs, the recycled forms account for 4–10% in the lower Goleugoed Formation, 2–6% in the upper Goleugoed Formation, and fall to less than 1% in the Rhydings Formation.

Appendix 2. Llandovery district locality numbers

Formations are given as: Tr = Tridwr, S = Scrach, B = Bronydd, Cr = Crychan, Co = Coldbrook, Ce = Cerig, Go = Goleugoed, Gw = Gwernfelen, Tf = Trefawr, R = Rhydings, W = Wormwood, D = Derwyddon.

The eight-figure numbers shown are the National Grid References of Great Britain; they all lie within the SN 100-km grid square.

3	8164	3798	Tf
4	8158	3760	R
5a	8171	3751	R
5b	8172	3751	W
6	8181	3756	W
7	8207	3795	Ce
8	8484	3888	Tr
9	8450	3898	S
10	8450	3912	S
11	8425	3912	B
12	8410	3901	Cr
13	8374	3902	Tf
14	8340	3891	R
15	8299	3831	R
16	7601	3102	Go
17	8151	3732	R
18	8119	3738	Tf
19	8090	3729	Tf
20	8491	4111	S
21	8501	4079	S
22	8502	4048	S
23	8481	3999	S
24	8458	3964	S
25	8468	3961	S
26	8456	3955	B
27	8451	3953	B
28	8448	3952	Cr
29	8442	3949	B
30	8466	3924	S
31	8471	3920	Tr
32	8423	3950	Cr
33	8414	3941	Cr
34	8407	3928	Cr
35	8397	3907	Cr
36	8327	3929	Tf
37	8265	3909	Tf
38	8391	3960	Tf (= 38s)
38b	8383	3956	Tf
38c	8367	3940	Tf
39	8363	3937	Tf
39a	8356	3931	Tf (= 40)
40	8356	3931	Tf
41	8410	3963	Cr
42	8440	3982	Cr
43	8299	3826	R
44	8288	3809	R
45	8300	3809	R
46	8302	3775	R
47	8263	3777	W
48	836	377	Cr
49	8335	3728	Tf
50	8357	3717	Cr
51	8361	3724	Cr
52	8379	3788	Cr
53	8389	3808	Cr
54	8390	3815	Cr
55	8443	3863	S
56	8428	3861	B
57	8421	3814	S
58	8420	3780	Tr
59	8109	3812	Co
60	8116	3808	Co
61	8458	3956	B
62	8439	3951	Cr
63	8422	3949	Cr
64	8420	3948	Cr
65	8417	3944	Cr
66	8403	3920	Cr
67	8371	3898	Tf
68	8415	3966	Cr
69	8405	3972	Cr
70	8385	3958	Tf
71	8382	3950	Tf
72	8380	3953	Tf
73	8372	3943	Tf
74	8371	3943	Tf
75	8368	3940	Tf
76	8347	3925	Tf
77	8360	3934	Tf
78	8132	3839	S
79	8128	3836	Co
80	8127	3835	Co
81	8121	3832	Co
82	8121	3806	Co
83	8128	3805	Tf
84	8203	3822	Tf
85	8369	4045	B
86	8367	4028	B
87	8361	4082	Tr
88	8459	3957	B
89	8343	3920	R
90	8376	4059	S
91	8286	3954	B
92	8323	3975	B
93	8433	4017	Cr
94	7516	3003	Go
95	7544	2972	Go
96	7460	2984	Tr
97	7552	3102	Go
98	7568	3086	Go
99	7888	3485	Co
100	8207	3837	Tf
101	8147	3771	R
102	8162	3756	R
103	8163	3754	R
104	7823	3326	R
105	7829	3325	W
106	7863	3314	Gw
107	7846	3318	Ce
108	7846	3338	W
109	7820	3334	R
110	8470	3902	Tr
111	8473	3902	Tr
112	8447	3867	S
113	8339	3766	Tf
114	8352	3776	Tf
115	8365	3787	Cr
116	8412	3709	B
117	8410	3717	B
118	8491	3725	D
120	7604	3091	Go
121	7643	3046	W
122	7441	2819	W
123	8532	3850	Ce
124	8473	3715	B
125	8475	3715	B
126	8477	3713	Cr
127	8479	3712	D
128	8480	3711	D
129	8489	3702	Ce
130	8538	3843	D
131	8546	3841	Ce
132	8558	3839	Tr
133	8551	3839	Tr
134	8562	3836	D
135	8658	3880	Gw
136	8599	3845	Ce
137	8343	3887	R
138	8348	3887	R
139	8153	3764	R
140	8188	3764	Ce
141	7760	3328	Co
142	7759	3326	Co
143	7758	3323	Co
144	7760	3374	Co
145	7766	3357	Co
146	7767	3354	Co
147	7514	3191	Go
148	7516	3191	Go
149	7529	3192	Go
150	7515	3072	Go
151	8383	3957	Tf
152	7756	3279	R
153	7756	3277	R
154	7754	3271	R
155	7750	3265	R
156	7749	3260	R
157	7749	3255	R
158	7749	3255	W
159	7744	3241	W
160	7745	3239	W
161	7744	3235	W
162	7742	3233	W
163	7746	3229	Ce
164	7767	3352	Co
165	7679	3328	Co
166	8378	3950	Tf
167	8375	3946	Tf
168	7418	2817	R
169	7418	2812	R
170	7595	2957	W
171	7993	3547	W
172	8011	3564	W
173	8006	3568	W
174	8008	3553	W
175	8091	3703	R
176	8193	3777	W
177	8190	3790	R
178	7534	3086	Go
179	7546	3107	Go
180	7550	3117	Go
181	7566	3086	Go
182	7571	3091	Go
183	7582	3114	Go
184	7610	3126	Go
185	7435	2808	Gw
186	8420	3949	Cr
187	7743	3231	W
188	7455	3022	S
189	7591	3277	S
190	7764	3365	Co
191	7425	3080	Go
192	7443	3074	Go
193	7767	3345	Co
194	7563	3230	Go
195	7513	3042	Go
196	7522	3050	Go
197	7531	3088	Go
198	7540	3203	Go
199	7535	3191	Go
200	7534	3178	Go
201	8363	3895	Tf
202	8363	3895	Tf
203	8362	3894	Tf
204	8360	3894	Tf
205	8358	3893	Tf
206	8356	3892	Tf
207	8364	3896	Tf
208	8366	3896	Tf
209	8367	3896	Tf
210	8441	3952	Cr
211	8375	3904	Tf
212	8373	3900	Tf
213	8251	3704	W
214	7550	3117	Go
215	7612	3116	Go
216	7755	3302	R
217	7756	3300	R
218	7753	3295	R
219	7756	3291	R
220	7758	3285	R
221	7752	3268	R
222	7904	3369	Gw
223	7730	3187	Ce
224	8449	3953	Cr

Note – Other sample numbers with a or b are from the same localities as the corresponding number without letter.

Appendix 3. Grid references of logged sections of transects

All lie within the SN 100 km grid square, and they are also shown on Figs 2, 3, 4 and 6.

Transect	base	top	Remarks
a	7415 2828	7450 2825	outcrops in banks of River Sefin
b1	7462 2980	7463 2981	Forestry Commission track
b2	7495 3005	7445 2974	Forestry Commission track
c	7496 3067	7548 3096	natural outcrops and quarry sections in Ydw valley
d1	7757 3388	7760 3375	stream section
d2	7763 3368	7768 3353	stream section
d3	7760 3325	7747 3230	road section and abandoned quarries near top
d4	7847 3318	7848 3302	stream section
f1	8108 3813	8115 3808	Forestry Commission track
f2	8208 3838	8192 3811	Forestry Commission track
f3	8160 3756	8192 3765	Forestry Commission track
g	8367 4070	8352 4006	Forestry Commission track
h	8391 3960	8342 3921	Forestry Commission track
i1	8474 3904	8467 3901	Forestry Commission track
i2	8467 3962	8398 3912	Forestry Commission track
i3	8376 3906	8343 3887	Forestry Commission track
j1	8422 3818	8414 3804	Forestry Commission track
j2	8335 3763	8373 3795	Forestry Commission track
k	8410 3720	8416 3700	Forestry Commission track
l	8464 3720	8489 3700	Forestry Commission track
m	8492 3740	8498 3725	Forestry Commission track
n	8550 3838	8558 3823	Forestry Commission track

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Accepted for publication 22 May 1984

British Museum (Natural History)

An account of the Ordovician rocks of the Shelve Inlier in west Salop and part of north Powys

By the late W. F. Whittard, F.R.S. (Compiled by W. T. Dean)

Bulletin of the British Museum (Natural History), Geology series
Vol. 33 No. 1. Dec. 1979. 69pp. 38 figs. Large full-colour map

The late Professor W. F. Whittard, F.R.S., who died in 1966, devoted much of his life to the study of the Shelve Inlier, and his great monograph on its trilobites remains fundamental. The area, in west Salop (including a small part of north Powys), was the scene of famous early geological studies by Murchison and Lapworth. By Palaeozoic standards it is in places richly fossiliferous, and exhibits the best continuous Ordovician succession in Britain, one which is indeed amost complete. This classic area is of continuing interest, not only to professionals but also to amateur geologists and students, few of whom complete their studies without at least one field visit; but amazingly this is the first detailed map ever to be published. That the work of Whittard, now made available through the efforts of Professor W. T. Dean of Cardiff, is authoritative there can be no doubt: for over thirty-five years he studied these rocks, unravelling their complexities and perfecting his map.

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Bulletin of the
British Museum (Natural History)

Lower Ordovician Brachiopoda from the Tourmakeady Limestone, Co. Mayo, Ireland

Alwyn Williams & Gordon B. Curry

Geology series Vol 38 No 4 31 January 1985

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World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Geol.)

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The Geology Series is edited in the Museum's Department of Palaeontology
Keeper of Palaeontology: Dr H. W. Ball
Editor of the Bulletin: Dr M. K. Howarth
Assistant Editor: Mr D. L. F. Sealy

ISBN 0 565 07003 7
ISSN 0007–1471

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Geology series
Vol 38 No 4 pp 183–269

Issued 31 January 1985

BRITISH MUSEUM (NATURAL HISTORY)
31 JAN 1985

Lower Ordovician Brachiopoda from the Tourmakeady Limestone, Co. Mayo, Ireland

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Synopsis

A study of fossil Brachiopoda collected from etched residues of the Upper Arenig Tourmakeady Limestone, Co. Mayo, Republic of Ireland, reveals the presence of 45 species (25 of them new) belonging to 41 genera of which 12 are new. The new inarticulate genera recognized are the lingulacean *Dictyobolus*, the acrotretacean *Mylloconotreta* (probably two species), and the siphonotretaceans *Cyrbasiotreta* and *Karnotreta*. The 8 new articulate genera comprise the orthaceans *Protohesperonomia, Lomatorthis, Notoscaphidia* and *Crossiskenidium* (two species); the clitambonitacean *Acanthotoechia*; the plectambonitaceans *Borua* and *Tourmakeadia* and the porambonitacean *Acanthoglypha*. The fauna additionally contains new species of *Lingulobolus, Lingulella, Conotreta, Ceratreta, Multispinula, Archaeorthis, Taphrorthis, Phragmorthis, Protoskenidioides, Pomatotrema, Leptella, Syntrophina* and *Porambonites*, as well as representatives of *Westonia, Plectoglossa* (?), *Acanthambonia, Elliptoglossa, Conotreta, Scaphelasma, Eoconulus, Schizotreta, Multispinula, Apheorthis, Orthidium, Nothorthis, Orthambonites, Tritoechia, Punctolira* (?) and *Idiostrophia*.

The Tourmakeady fauna shows strong North American affinities, with only one of the established genera not previously recorded in Upper Cambrian or Lower and Middle Ordovician successions from that continent.

Introduction

This paper is a systematic study of the brachiopod remains recovered from the Lower Ordovician Tourmakeady Limestone and associated rocks exposed in Co. Mayo, Republic of Ireland. Although the geology of the Lower Ordovician inliers in the Tourmakeady and Glensaul districts was first described in detail by Gardiner & Reynolds (1909, 1910), the abundance of the shelly fossils was not then appreciated and the rich assemblages have never been subjected to full taxonomic investigation. Gardiner & Reynolds did, however, recognize the stratigraphical importance of the inliers, and their age determinations were based on lists of graptolitic and shelly faunas collected from various exposures within the Tourmakeady and Glensaul successions. The graptolite faunas have been reinvestigated

(Dewey *et al.* 1970), but up to now the shelly fossils have been known only from two brief palaeontological accounts by Reed (*in* Gardiner & Reynolds 1909, 1910), describing six brachiopod species.

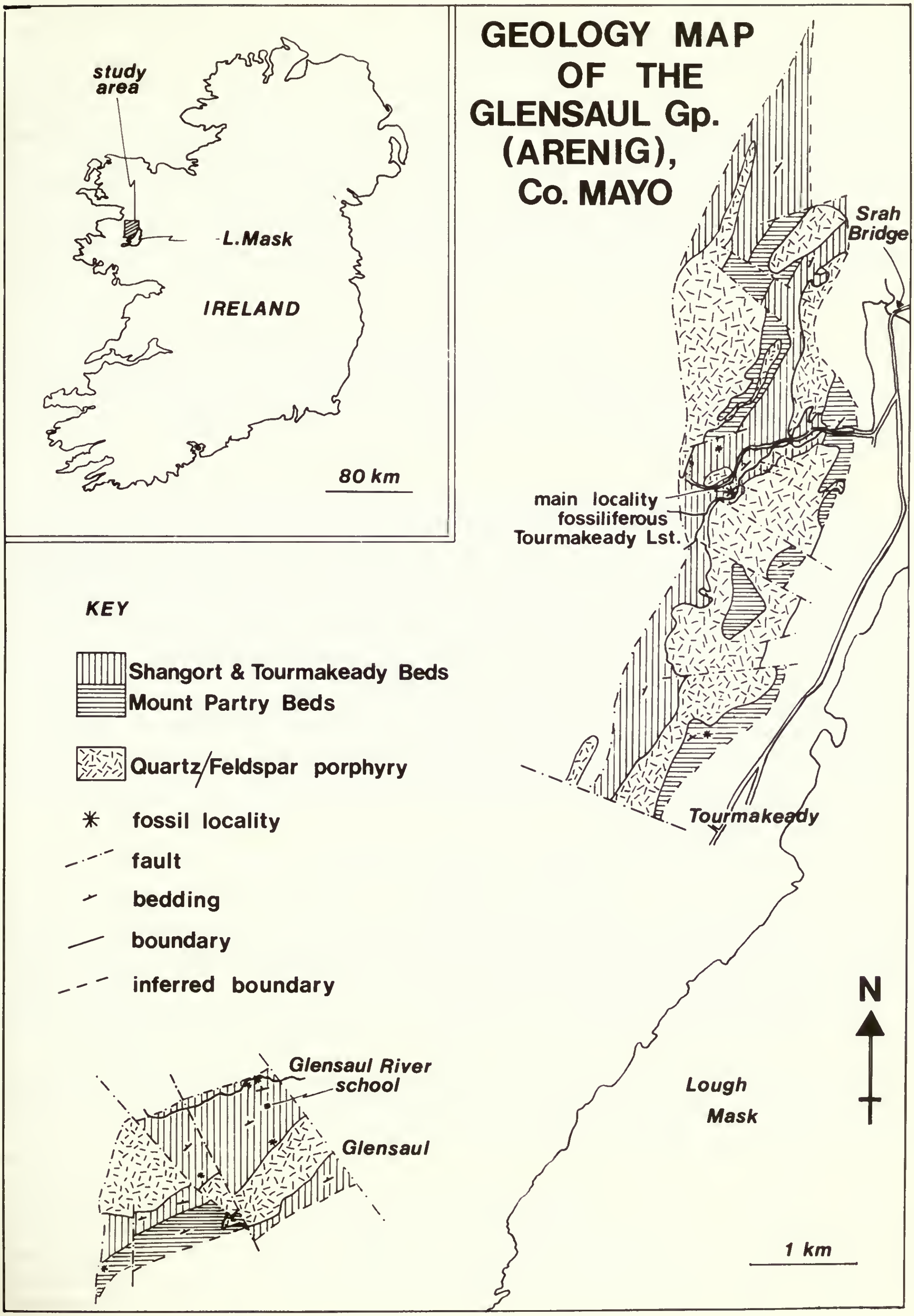
Intensive collecting, which furnished the material for the present study, began in 1963 when it was discovered that the skeletal remains of many phyla represented in the richly fossiliferous Tourmakeady Limestone had been silicified. Bulk sampling and acid etching of over two tons of limestone revealed an early Ordovician brachiopod fauna of unprecedented diversity, much of it previously undescribed. Moreover, other phyla were well represented in the etched residues and are now being described. In due course this study will be complemented by a description of the Tourmakeady trilobites by R. A. Fortey, and by illustrations of other rarer but still important groups, notably bryozoans, gastropods and crinoids, thereby completing the taxonomy of a major fauna which is significant not only because of its abundance, preservation, and diversity, but also because of the information it provides on Lower Ordovician biogeography.

The Tourmakeady Limestone occurs in isolated blocks within well-bedded calcareous tuffs and grits. Together these lithologies constitute the 'Shangort and Tourmakeady Beds' of Gardiner & Reynolds, a term retained herein (Fig. 1) although rigorous application of stratigraphic procedure, beyond the scope of this work, would require the establishment of more precisely defined formational units. The shelly fossils indicate an Upper Arenig age for the Tourmakeady Limestone, equivalent to Zone K of the North American biostratigraphical succession (see table in Curry *et al.* 1982). This is consistent with the graptolite evidence, which includes an uppermost Lower Arenig assemblage ascribed to the *Isograptus gibberulus* Zone near the base of the Shangort and Tourmakeady Beds, and an Upper Arenig assemblage indicative of the *Didymograptus hirundo* Zone for a new locality at the top of the Formation (Gardiner & Reynolds 1909, 1910; Dewey *et al.* 1970). The underlying Mount Partry Beds have yielded Lower Arenig graptolites (*D. nitidus* Zone), confirming that the age span of the successions of the Tourmakeady and Glensaul inliers, which together constitute the Glensaul Group (Williams *et al.* 1972), lies entirely within the Arenig.

The Tourmakeady Limestone fossils have also been recovered from several exposures of the enclosing calcareous tuffs in both inliers (Fig. 1) and, although less well preserved than the etched specimens, are clearly conspecific, and almost certainly contemporaneous. The disjunct outcrops of the Tourmakeady Limestone suggest that the Member was initially in more continuous sheets along the postulated fault-controlled southern margin of the 'South Mayo Trough', but was fractured and dislocated shortly after lithification, and then rafted as dispersed blocks at a time when contemporaneous vulcanicity was generating considerable quantities of quartz and feldspar porphyry and feeding submarine flows of tuffs and associated clastic sediments.

The brachiopods from the Tourmakeady Limestone display strong North American affinities. Excluding new genera, over 50% of the Tourmakeady genera were included by Ulrich & Cooper (1938) in their survey of Upper Cambrian and Lower Ordovician brachiopods from North America, while a further 45% of the previously-established Tourmakeady genera occur in younger Ordovician successions in that continent (Cooper 1956). Nearly a third of the brachiopod genera occurring in the richly fossiliferous Lower Ordovician Antelope Valley Limestone at Meiklejohn Peak, Nevada (Ross 1972; Krause & Rowell 1975) are represented in the Tourmakeady Limestone. Such correlation, which emphasizes the faunal continuity within the Scoto-Appalachian (or American) Province (Williams 1969), contrasts markedly with comparisons between the Tourmakeady faunal lists and those from outcrops within other Lower Ordovician faunal provinces (Williams 1973). Thus out of 28 genera recorded from Arenig successions (Celtic province) in New World Island (Neuman 1976) only *Multispinula, Orthambonites* and *Tritoechia* are common to the

Fig. 1 Summary geological map of the Tourmakeady–Glensaul districts, Co. Mayo, Republic of Ireland, showing fossil location referred to as Loc. 1 in text.


GEOLOGY MAP OF THE GLENSAUL Gp. (ARENIG), Co. MAYO
study area
L. Mask
IRELAND
80 km
Srah Bridge
main locality fossiliferous Tourmakeady Lst.
KEY
Shangort & Tourmakeady Beds
Mount Partry Beds
Quartz/Feldspar porphyry
fossil locality
fault
bedding
boundary
inferred boundary
Tourmakeady
Glensaul River
school
Glensaul
Lough Mask
N
1 km

Mayo successions. The last two genera are again the only taxa found in both the Tourmakeady Limestone and in early Ordovician rocks from Anglesey, North Wales (Neuman & Bates 1978). Recent descriptions of the Lower Ordovician faunas from the Montagne Noire, France (the Anglo-French province), reveals only one common articulate (*Orthambonites*) and three inarticulate genera (Havlíček 1980, Babin *et al.* 1982) out of a total fauna of 17 genera. Similarly, the distinction between the Tourmakeady fossils and those from contemporaneous rocks within the Baltic province is equally apparent (e.g. Neuman & Bruton 1974, Bruton & Harper 1981). In view of the pandemic distribution of *Orthambonites* and *Tritoechia*, it seems reasonable to assume that the many new taxa described in this paper were really part of the benthic faunas of the American Province and have yet to be discovered in association with the better-known species outside County Mayo.

Type locality and horizon

Unless otherwise stated, the type horizon and locality of all new species we describe herein is: Tourmakeady Limestone; banks of un-named stream, 2 km south-west of Srah Bridge, Co. Mayo, Republic of Ireland (Loc. 1; Grid reference M 105719). See Fig. 1.

Systematic methods and terminology

The recovery of large numbers of isolated complete valves from the Tourmakeady Limestone provides the means to augment standard qualitative systematic procedures with bivariate analysis of the shell parameters normally used for taxonomic differentiation. Standardization of the statistical methodology utilized in such analyses, and of the method of data presentation, allows comparisons with other samples, and also provides a rigorous framework for assessing evolutionary trends. Accordingly the statistical procedures adopted herein are those used in other studies of Ordovician brachiopods (e.g. Williams 1974, Lockley & Williams 1981). The taxonomic weight given to statistically significant differences in skeletal morphology is that described by Williams (1962: 70–79). In addition the resulting data have been presented in the same way as those used by Lockley & Williams (1981). The mean, variance and number of measurements have been incorporated directly into the systematic descriptions, and when expressed as bivariates are accompanied by the appropriate coefficients of correlation (r).

The following abbreviations have been used in the text, referring to shell features measured in millimetres: l ($\bar{l}$) maximum length (and mean); w ($\bar{w}$) maximum width (and mean); th ($\overline{th}$) maximum shell depth (and mean); l_s ($\bar{l}_s$) maximum length of median septum or ridge (and mean); l_{sc} ($\bar{l}_{sc}$) maximum length of muscle scars (and mean); l_{te} ($\bar{l}_{te}$) maximum length of teeth (and mean); l_b ($\bar{l}_b$) maximum length of brachiophores or brachiophore bases (and mean); w_{so} ($\bar{w}_{so}$) maximum width of socket ridges (and mean); l_n ($\bar{l}_n$) maximum length of notothyrial platform (and mean); l_p ($\bar{l}_p$) maximum length of pseudospondylium (and mean); l_{sp} ($\bar{l}_{sp}$) maximum length of spondylium (and mean); l_{in} ($\bar{l}_{in}$) maximum length of interarea (and mean); l_{lp} ($\bar{l}_{lp}$) maximum length of lophophore platform (and mean).

All specimens have been deposited in the British Museum (Natural History). The registration numbers quoted in the text, with the prefix BB, refer to the fossil Brachiopoda collections in the Department of Palaeontology of that institution.

Taxonomic descriptions

Class **INARTICULATA** Huxley, 1869

Order **LINGULIDA** Waagen, 1885

Superfamily **LINGULACEA** Menke, 1828

Family **OBOLIDAE** King, 1846

Subfamily **OBOLINAE** King, 1846

Genus ***DICTYOBOLUS*** nov.

DIAGNOSIS. Convexo-plane to unequally biconvex obolids, with truncated posterior margins, young valves semicircular in outline becoming transversely oval in later stages of growth with more obtuse cardinal extremities; shell surface ornamented by distally rounded, slightly everted concentric lamellae and two superimposed sets of obliquely-disposed fine ridges intersecting in an acutely rhombic microscopic pattern.

Ventral interior with strong, apsacline pseudointerarea divided into narrowly triangular propareas by a pedicle groove consisting of a sunken concave plate with free, rounded anterior margins; muscle scars forming arc of oblique and median impressions interrupted by divergent *vascula lateralia.*

Dorsal interior with anacline pseudointerarea thickened and indented medially by a broad shallow depression; muscle impressions unknown.

NAME. Greek, *δίϰτῠον*, a net.

TYPE SPECIES. *Dictyobolus transversus* sp. nov. from the Tourmakeady Limestone, Co. Mayo.

DISCUSSION. The combination of transversely oval shape, elevated concentric ornamentation, and strong divided pseudointerareas in both valves, indicates that the obolid *Dictyobolus* is most appropriately assigned to the Obolinae. Within that subfamily *Dictyobolus* is readily distinguishable from all other obolines by the presence of the sunken median plate in the ventral pseudointerarea, and its distinctive ornamentation. In shape, *Dictyobolus* is comparable to *Obolus* Eichwald and *Thysanotos* Mickwitz, but *Obolus* has a narrow pedicle groove and lacks strong concentric ornamentation, whilst the elevated ornamentation of *Thysanotos* bears regular rows of fine spines.

Differences in ornamentation and in the structure of the ventral and dorsal pseudointerarea serve to distinguish *Dictyobolus* from *Dicellomus* Hall and *Pseudodicellomus* Bell.

Palaeobolus Matthew and *Aulonotreta* Kutorga also have elevated concentric ornamentation which, however, differs from that of *Dictyobolus* in being discontinuously developed, especially in *Aulonotreta*. In addition, both genera have elongate, strongly biconvex shells which immediately distinguish them from *Dictyobolus*.

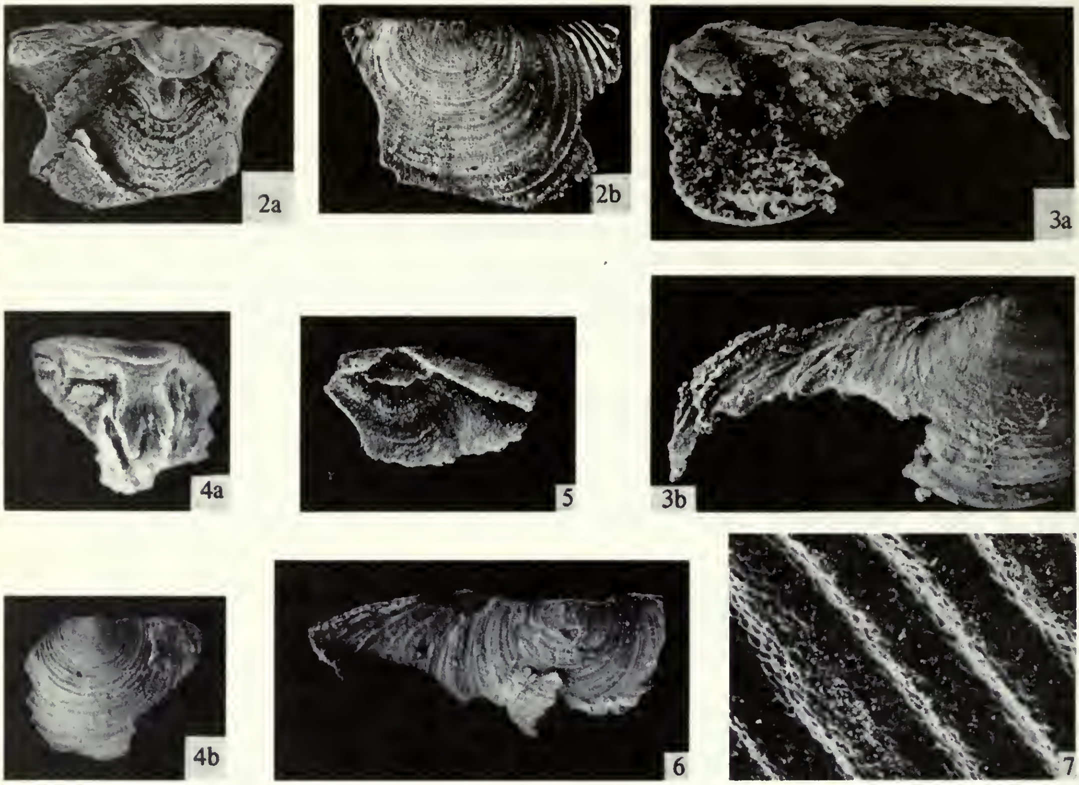
Dictyobolus transversus sp. nov.

Figs 2–7

DIAGNOSIS. Thick-shelled *Dictyobolus* ornamented by concentric lamellae with wavelength and amplitude of 0·1 mm at 2 mm anterior of ventral umbo, and two intersecting sets of fine ridges forming acutely rhombic pattern with dimensions of $70 \times 25\,\mu m$ medially; composite arcuate muscle scar, convex anteriorly, impressed posteromedially in the pedicle valve.

NAME. 'Crosswise'.

DESCRIPTION. Medium-sized convexo-plane to unequally biconvex *Dictyobolus*, estimated to have attained a maximum length and width of *c.* 7·5 mm and 12 mm respectively. Juvenile shells semicircular, about 85% as long as wide, becoming transversely oval in later growth stages and 65% as long as wide; cardinal extremities of truncated posterior margin obtusely rounded at 150°, anterior margins of valves rectimarginate, truncated, becoming smoothly rounded anterolaterally; ornamented by strong, elevated concentric lamellae rounded distally and everted slightly posteriorly, with wavelength and amplitude of 0·1 mm at 2 mm anteromedially of ventral umbo; lamellae in adult shells most strongly developed anteromedially and anterolaterally, with wavelengths up to 0·4 mm and amplitudes up to 0·3 mm and commonly interspersed with secondary lamellae; external valve surfaces further ornamented



Figs 2–7 *Dictyobolus transversus* gen. et sp. nov. Fig. 2a, b, **holotype** BB 95387, interior and exterior of incomplete pedicle valve, both ×7; Fig. 3a, b, paratype BB 95391, interior and exterior of incomplete pedicle valve, both ×6; Fig. 4a, b, paratype BB 95392, interior and exterior of incomplete brachial valve, both ×6; Fig. 5, paratype BB 95389, interior of pedicle valve, ×7; Fig. 6, paratype BB 95388, exterior of incomplete pedicle valve, ×6; Fig. 7, paratype BB 95519, detail of external ornamentation, ×90.

by two sets of obliquely-disposed fine ridges with wavelength of $25\,\mu m$ and amplitude of $5\,\mu m$, intersecting to form acutely rhombic pattern about $70 \times 25\ \mu m$ medially.

Interior of pedicle valve with thickened apsacline pseudointerarea divided into narrowly triangular propareas by shallowly concave pedicle groove, propareas strongly grooved by growth-lines, especially posterolaterally; pedicle groove defined by broad, semicircular, sunken plate ankylosed with floor of valve posteriorly but becoming free anteriorly and anterolaterally, plate finely grooved by concentric growth-lines and 57% as long as wide in two specimens; composite arcuate muscle scars, convex anteriorly and 39% as long as wide in two specimens impressed posteromedially but interrupted by divergent branches of *vascula lateralia*; paired median muscle scars symmetrically disposed about median axis of valve and separated from posterolaterally-situated oblique muscles by canals of *vascula lateralia* about 2 mm wide, axes of *vascula lateralia* diverging anteriorly at angle of 35° to median axis of valve.

Dorsal pseudointerarea wide, thickened, anacline, and divided into well-defined propareas by broad, shallowly concave, median depression 2·6 mm wide; shell strongly thickened posteriorly, rising up to buttress elevated anterior margin of median depression.

HOLOTYPE. Incomplete pedicle valve, BB 95387. Fig. 2.

PARATYPES. Incomplete pedicle valves, BB 95389–91; incomplete brachial valves, BB 95388, 95392; fragments, BB 95519–20.

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. The new genus *Dictyobolus* is at present monospecific, and only known from over 80 incomplete specimens recovered from the etched residues from the Tourmakeady Limestone. Among described species, only *Obolus* sp. 3 from the Pratt Ferry Formation of Alabama (Cooper 1956: 163) has the transversely oval shape and strong elevated concentric ornamentation characteristic of *D. transversa* and may well belong to the new genus. The internal structures of this species are, however, unknown, and there is no record of the superimposed pattern of intersecting fine ridges so characteristic of the Irish genus.

Genus ***LINGULOBOLUS*** Matthew 1895

Lingulobolus septatus sp. nov.

Figs 8–10

DIAGNOSIS. Strongly biconvex *Lingulobolus* lacking radial ornamentation and internally with short median septum and two short lateral septa anterior of the pedicle groove.

NAME. 'With septa'.

DESCRIPTION. Medium-sized, elongately oval dorsibiconvex *Lingulobolus* attaining maximum size of 10–12 mm; external surfaces with rare, fine concentric growth-lines; pedicle valve with subacuminate posterior margin, moderately convex medially becoming less convex peripherally; posterior margin of brachial valve obtusely rounded; shell substance lamellar.

Interior of pedicle valve with broadly triangular pseudointerarea, strongly thickened medially and divided into small triangular propareas by broad triangular pedicle groove; propareas thin-shelled, elevated above valve floor, and forming dorsal margins of deep umbonal cavities approximately 0·5 mm in maximum diameter; pedicle groove shallowly concave, about 50% as wide as long in two specimens, with strongly thickened anterior margin ankylosed with, and elevated above, floor of valve; pedicle groove buttressed anteriorly by short median septum and two short lateral septa; paired, broadly oval, transmedian muscle scars shallowly impressed on floor of valve lateral of median septum; single circular pedicle muscle (?) scar impressed anteromedially on pedicle groove.

Dorsal pseudointerarea narrow, undivided, and recurved posteromedially; floor of brachial valve with broad, low, narrowly triangular median septum first discernible about 0·5 mm anterior of pseudointerarea and becoming progressively wider and thicker anteriorly; median septum slightly bilobed anteriorly, with superimposed low, rounded, median ridge up to 0·3 mm wide; strong, paired, oval transmedian muscle scars (presumably associated with outside and middle laterals) impressed posterolateral of the posterior margin of the median septum; anterior to these another pair of scars probably representing central muscle bases; narrow depression immediately anterior of medium septum probably the attachment site of anterolateral muscles; paired umbonal muscles, tear-shaped and about three times as long as wide, deeply impressed anterolaterally of dorsal pseudointerarea, margins of umbonal muscle scars defined posteriorly by narrow, slightly elevated, ridge of shell, and anteriorly by strongly-developed, posteriorly-reclining anteromedian wall strongly thickened posteriorly; muscle scar bases grooved by growth-lines.

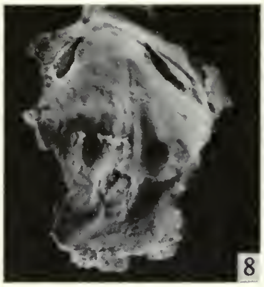
HOLOTYPE. Incomplete brachial valve, BB 95397. Fig. 8.

PARATYPES. Incomplete pedicle valve, BB 95398; incomplete brachial valve, BB 95399.

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. Differences in shape, external ornamentation, and internal structure of the pedicle valve serve to distinguish *L. septatus* from all described species of this rare genus.

L. spissus (Billings) from the Lower Ordovician of Newfoundland (Walcott 1912: 432) is similar to *L. septatus* in being dorsibiconvex and, in the brachial valve, in having strong umbonal muscle scars and a broad, low, median septum flanked by deeply impressed muscle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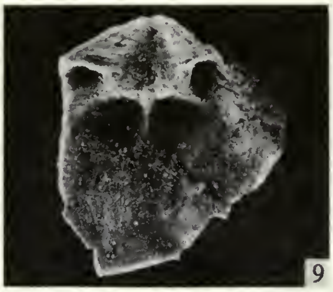
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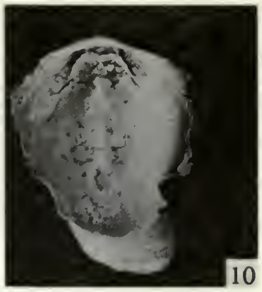
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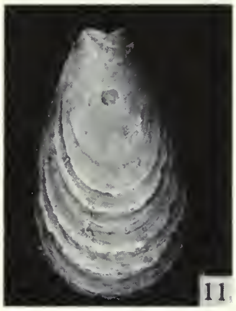
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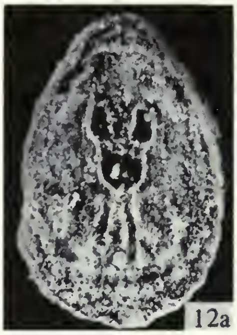
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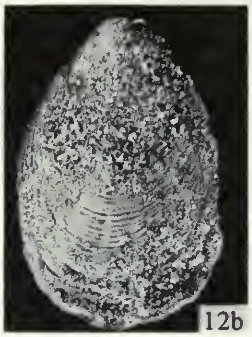
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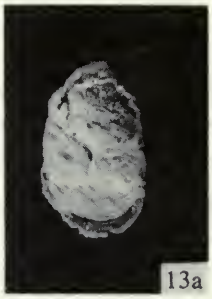
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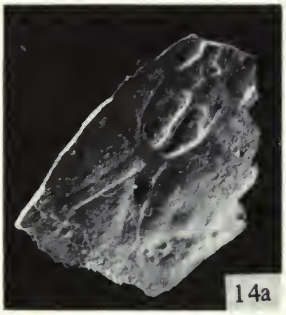
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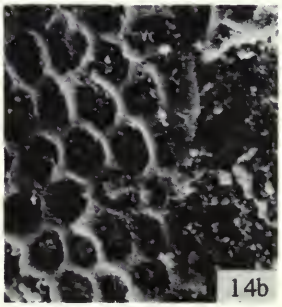
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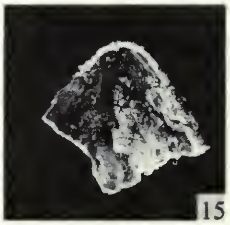
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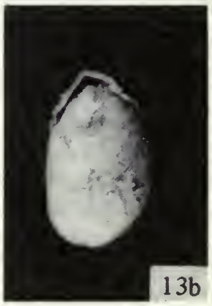
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Figs 8–10 *Lingulobolus septatus* sp. nov. Fig. 8, **holotype** BB 95397, interior of incomplete brachial valve, ×6; Fig. 9, paratype BB 95398, interior of incomplete pedicle valve, ×7; Fig. 10, paratype BB 95399, interior of incomplete brachial valve, ×4.

Figs 11–15 *Lingulella hespera* sp. nov. Fig. 11, **holotype** BB 95393, exterior of incomplete pedicle valve, ×5; Fig. 12a, b, paratype BB 95395, interior and exterior of pedicle valve, both ×7; Fig. 13a, b, paratype BB 95394, dorsal and ventral views of juvenile conjoined valves, both ×12; Fig. 14a, b, paratype BB 95475, interior of incomplete pedicle valve: a, ×15; b, detail of epithelial moulds on shell interior, ×640; Fig. 15, paratype BB 95396, interior of incomplete brachial valve, ×8.

scars. The structure of the dorsal pseudointerarea is also similar in both species, being narrow and recurved posteriorly. However, *L. septatus* differs from the Canadian species in having median and lateral septa in the pedicle valve, and in the absence of radial ornamentation externally.

L. septatus can readily be distinguished from *Obolus* (*Lingulobolus*) *affinis* (Billings), also from the Lower Ordovician of Newfoundland (Walcott 1912: 433), as the latter is triangular in shape, has strong external radial ornamentation, and lacks septa in the pedicle valve.

Lingulobolus has also been recorded from Europe. *Obolus* (*Lingulobolus*) *feistmanteli* (Kohila) from the Lower Ordovician of Poland, according to poorly illustrated material figured by Bednarčzyk (1964), differs from *L. septatus* in having a much more acuminate posterior margin, a wider dorsal pseudointerarea, and umbonal muscle scars situated much closer to the median axis of the brachial valve. *L. brimonti* (Rouault) from the Lower Ordovician of France and ? north Africa (Havlíček 1980: 3) and *L. hawkei* (Rouault) from the Lower Ordovician of France and Lower Ordovician pebbles in the Triassic Budleigh Salterton Pebble Bed of England (Davidson 1866: 41; Cocks & Lockley 1981: 113) have much stronger concentric ornamentation, and also differ from *L. septatus* in internal morphology.

Subfamily **LINGULELLINAE** Schuchert 1893

Genus ***LINGULELLA*** Salter 1866

Lingulella hesperia sp. nov.

Figs 11–15

DIAGNOSIS. Subtriangular *Lingulella* broadening to almost three-fifths as wide as long in anterior half of shell, anterior margin rounded, lateral margins gently rounded, tapering to become progressively acuminate posteriorly.

NAME. ‘Western’.

DESCRIPTION. Medium-sized elongately subtriangular biconvex *Lingulella* 57% as wide as long in two specimens and attaining lengths of at least 7–8 mm; shell with maximum width anteriorly and tapering smoothly posteriorly; lateral margins of valves smoothly rounded and subparallel, especially in juvenile stages of growth; external ornamentation consisting of variably developed concentric growth-lines and fine, evenly-spaced, concentric fila numbering 12–16 per mm.

Pedicle valve moderately to strongly convex with sharply tapering subacuminate posterior margin and smoothly rounded anterior margin; pseudointerarea adnate with triangular propareas defined by weak flexure lines, propareas separated by broad pedicle groove up to 0·4 mm wide and only slightly elevated above valve floor, pedicle groove and propareas marked by fine growth-lines, anterior margins of propareas thin-shelled, slightly elevated above valve floor, and extended anteromedially as small semicircular lobes 0·2 mm in diameter; two sets of longitudinally ovate muscle scars, with dimensions of 0·7 × 0·4 mm and 0·5 × 0·2 mm in two specimens, strongly impressed symmetrically on either side of median axis of valve, posteriormost set of muscle scars tapering sharply posteriorly and slightly bilobed anteriorly, with lateral separation of 0·5 mm and 0·4 mm in two specimens as compared with 0·1 mm for anterior pair in both specimens; two sets of aligned, elongately oval, cardinal muscle scars, with dimensions of 0·5 × 0·25 mm, deeply impressed slightly anterior of propareas; *vascula lateralia* as two parallel-sided canals, 1 mm long × 0·1 mm wide, strongly impressed anteriorly of muscle field, flanking faint elongate tear-shaped median depression; canals diverging anteriorly at 20° to median axis of valve.

Brachial valve moderately to strongly convex with rounded acuminate posterior margin and smoothly rounded anterior margin; dorsal pseudointerarea anacline, undivided, very narrow in juveniles but becoming wider, thickened, and posteriorly truncated (?) in adults.

HOLOTYPE. Incomplete pedicle valve, BB 95393. Fig. 11.

PARATYPES. Conjoined juvenile valves, BB 95394a, b (length 2·7 mm, width 1·6 mm). Pedicle valve, BB 95395 (length 5·8 mm, width 3·2 mm); incomplete pedicle valves, BB 95475, 95521. Incomplete brachial valve, BB 95396.

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. Three *Lingulella* species from the Ordovician of North America have a broadly similar outline to that of the Tourmakeady specimens. They are *L. vermontensis* Ulrich &

Cooper, from the Providence Island Limestone of Vermont (Ulrich & Cooper 1938: 51), *L. lirata* from the Pratt Ferry Formation of Alabama (Cooper 1956: 201), and *L. spicata* Cooper from the Whitesburg Formation of Tennessee (Cooper 1956: 204). However, all three species, which are much larger than *L. hesperia*, have a much more acuminate posterior margin and a much narrower pedicle groove. Other species of *Lingulella* are less triangular in outline and also differ in other features. For example, *L. hesperia* can additionally be distinguished from *L. bullata* Krause & Rowell (1975: 15), from the Ordovician Antelope Valley Limestone in southern Nevada, in that the latter has a narrow submarginal ridge in both valves. The pedicle groove of *L.* cf. *zeuschneri* Bednarčzyk from the Tremadoc of Poland (Biernat 1973: 56) is much narrower than that of the Irish species, and the posterior margin of the pedicle valve is more strongly acuminate. *L.* (*Leptembolos*) *lingulaeformis* (Mickwitz) from the Cambro-Ordovician of the Russian Platform (Goryanskyiĭ 1969: 38) has a tapering subacuminate posterior margin similar to that of *L. hesperia*, but is much broader anteriorly.

The heterogeneous nature of the shell fabric of *Lingulella* may explain the variable degree of convexity of the Tourmakeady valves (Curry & Williams 1983). In living *Lingula* the different coefficient of contraction of the apatite as compared to the organic layers of the valves frequently results in strong distortion of the shell profile in dried specimens. Similar distortions are found in some of the Irish valves are excessively arched about the long median axis.

Genus *WESTONIA* Walcott, 1901

Westonia sp.

Figs 16–17

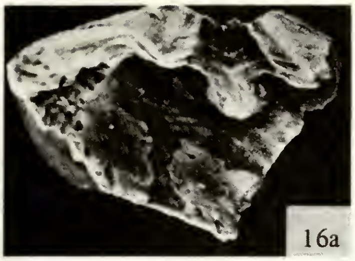
Diagnosis. Broadly oval (?) *Westonia* with truncated posterior margin to pedicle valve, open, reticulate ornamentation, and low, tongue-like, platform extending anteriorly of pedicle groove.

Description. Residues from etched blocks of Tourmakeady Limestone have yielded a few fragments of an inarticulate species, including a well-preserved posterior portion of a pedicle valve, all characterized by the distinctive external ornamentation of *Westonia*. Reconstructions suggest that the convex valves were broadly oval in outline, and approximately 15–18 mm long. The external surfaces are ornamented with rare, strong, concentric growth-lines, and two sets of narrowly rounded rugae with a wavelength of approximately 0·25 mm and an amplitude of approximately 0·75 mm at 3 mm anterior of umbo. Each set curves obliquely across the valve surface from the posterolateral margin to intersect with the opposite anterolateral margin at approximately 30°–50°. The intersection of these two sets of rugae gives rise to a delicate, lace-like, reticulate pattern. The pattern is first discernible about 2 mm anterior of the umbo, and the reticulations, commonly with curved posterior borders thickened at the junction, are approximately 0·2 mm square in the median region of the valve, 3 mm anterior of the ventral umbo.

In the interior of the pedicle valve the ventral pseudointerarea is wide, grooved by growth-lines, and divided into well-defined propareas by a shallow pedicle groove about 1·6 mm wide. The propareas are swollen immediately lateral to the pedicle groove and project anteriorly as a pair of rounded platforms. The triangular pedicle groove extends anteriorly as a broad, tongue-shaped plate ankylosed with the floor of the valve.

Figured material. Incomplete pedicle valve, BB 95384; incomplete valve, BB 95385. Loc. 1.

Discussion. Several *Westonia* species have been recorded from the Cambro-Ordovician successions of North America, but only *W. superba* Cooper and *W.* sp. 1 (Cooper 1956: 209) have an ornamentation comparable with the Irish material, albeit with more strongly developed rugae. The Tourmakeady *Westonia* can readily be distinguished from *W. linguloides* (Kobayashi), from the Upper Cambrian Limestones of Alaska (see Ulrich &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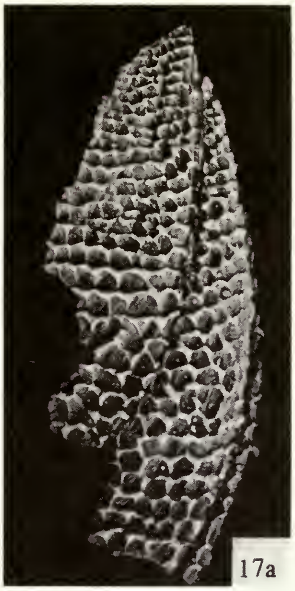
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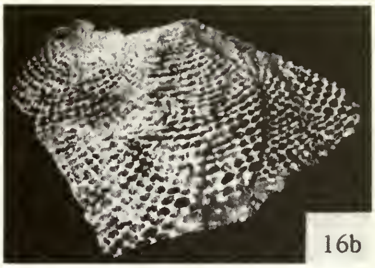
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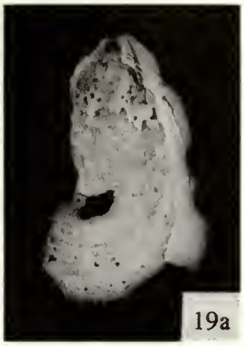
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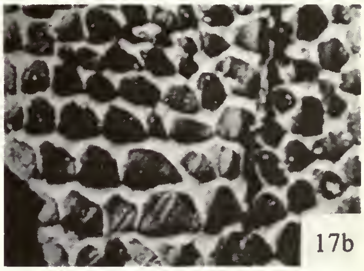
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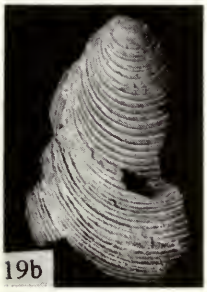
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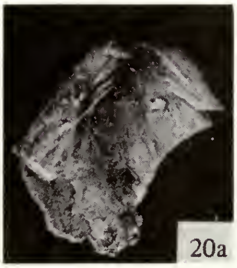
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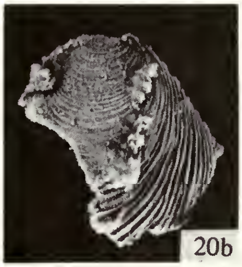
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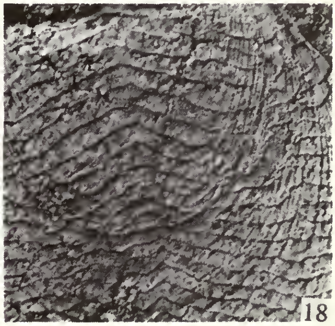
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Figs 16–17 *Westonia* sp. Fig. 16a, b, BB 95384, interior and exterior of incomplete brachial valve, ×7; Fig. 17a, b, BB 95385, exterior of fragment: a, ×10; b, ornamentation ×30.

Fig. 18 *Westonia ollius* (Whitfield). St Croix Sandstone, Wisconsin, U.S.A. USNM 27394, latex peel of exterior, ×10.

Figs 19–20 *Plectoglossa* sp. Fig. 19a, b, BB 95406, interior and exterior of incomplete pedicle valve, both ×4; Fig. 20a, b, BB 95407, interior and exterior of incomplete pedicle valve, both ×7.

Cooper 1938: 56), and *W. pupyshevi* Popov, from the Ordovician of Kazakhstan (Popov 1980: 84), both of which have a different ornamentation and a tapering triangular posterior margin to the pedicle valve. *Westonia* has also been described from the Cambro-Ordovician of the Russian Platform (Goryanskiĭ 1969: 40), and the Arenig of Estonia (Biernat 1973: 57). In both cases the pattern of ornamentation and shape of the ventral umbo are different, and there is no plate anterior to the pedicle groove.

The external ornamentation of *Westonia* is commonly described as being 'distinguished by peculiar, transverse, semi-imbricating, "ripple-embossed" lines that cross both concentric and radial striae' (Walcott 1912: 378). This is in contrast to the two oblique sets of rugae on the Irish *Westonia*. Moreover the development of a transverse ornamentation at right angles to the median axis of the valve and cutting across growth-lines is very difficult to rationalize in terms of the concentric growth of the valve margin. However, a detailed examination of some Upper Cambrian *Westonia* has indicated that the transverse ornamentation may be an artefact. For example, flattened specimens of *W. ollius* (Whitfield) from the St Croix Sandstone of Wisconsin (Walcott 1912: 465, figured on pl. XLIX as *W. stoneanus*) do indeed have a variably-developed transverse ornamentation of small scarps, forming either an irregularly transverse or zig-zag pattern medially (see Fig. 18). This pattern can be produced by the compression, during diagenesis, of convex shells composed of thin layers of apatite which can move slightly relative to one another on interleaved organic sheets and which break along crystallographically defined lines. However, a close inspection of valve surfaces of *W. ollius* also reveals two oblique sets of rugae (Fig. 18), each running obliquely across the valve from the posterolateral margin to the opposite anterolateral margin, exactly as described for the Irish *Westonia*. It seems probable, therefore, that the diagnostic ornamentation of undeformed *Westonia* consists of oblique rugae unaccompanied by transverse components.

Subfamily **GLOSSELLINAE** Cooper, 1956

Genus ***PLECTOGLOSSA*** Cooper, 1956

Plectoglossa ? sp.

Figs 19–20

Several fragments and a few incomplete valves of a distinctively ornamented glosselline species have been recovered from the Tourmakeady Limestone at Loc. 1, which are provisionally assigned to *Plectoglossa*. The largest specimen (BB 95406), a broken pedicle valve estimated to have been about 10 mm long and 7·5 mm wide when complete, has a tapering posterior margin and smoothly rounded anterior and lateral margins. On the basis of the available material it appears that the pedicle valve is gently and smoothly convex in lateral profile, and moderately to strongly convex in anterior profile. The external ornamentation is very distinctive, with prominent, evenly-spaced, elevated concentric fila averaging 5 per mm (range 4–6) over the postneanic surface of the valve. On the interior of the pedicle valve the ventral pseudointerarea is thickened, grooved by growth-lines, and divided into a pair of narrowly triangular propareas by strong flexure lines. The ventral propareas are separated by a broadly triangular, flat-lying, concave pedicle groove. Confirmation of this arrangement is seen on another incomplete pedicle valve assignable to the species (BB 95407).

In size, shape, and external ornamentation the Tourmakeady specimens are similar to typical *Plectoglossa* (Cooper 1956: 222) from the Ordovician of North America. However, the median fold in the pedicle groove which is said to be diagnostic of the genus is not evident in any of the pedicle valve fragments recovered from the Tourmakeady residues. Although the Irish material is somewhat abraded, it is not conceivable that this feature has been obscured by erosion, but in view of the inadequate sample it seems wiser to withhold full taxonomic recognition for the present, and provisionally to assign the specimens to *Plectoglossa* on the basis of the clear external similarities outlined above.

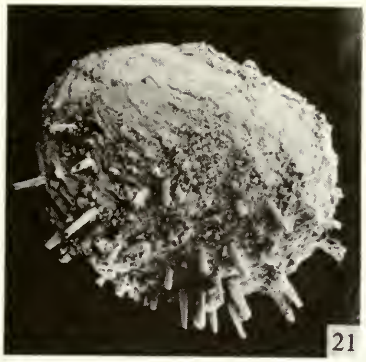
Subfamily **ACANTHAMBONIINAE** Cooper, 1956

Genus *ACANTHAMBONIA* Cooper, 1956

Acanthambonia sp.

Figs 21–22

The Tourmakeady Limestone exposed at Loc. 1 yielded two examples of the rare obolid genus *Acanthambonia*. The specimens (BB 95445–46) are almost circular in outline, the larger measuring 3·2 mm in length and 3·1 mm in width, with smoothly rounded lateral and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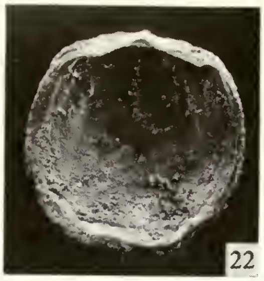
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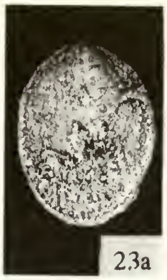
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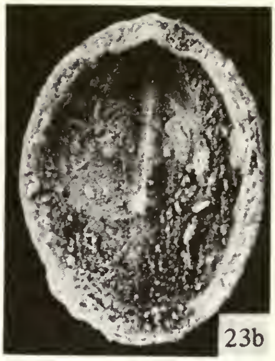
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Figs 21–22 *Acanthambonia* sp. Fig. 21, BB 95446, exterior of brachial valve, ×14; Fig. 22, BB 95445, interior of brachial valve, ×9.

Fig. 23a, b *Elliptoglossa* sp. BB 95405, exterior and interior of brachial valve: a, ×3; b, ×5.

anterior margins. The posterior margin is gently rounded and slightly truncated. In lateral profile the valves are moderately convex. The external surfaces are ornamented by fine concentric growth-lines and scattered, hollow, erect spines with a maximum diameter of 100 μm. On the interior of the brachial valve the dorsal pseudointerarea is well developed, and folded medially to form a rounded, convex, ridge.

In shape, disposition and size of external spines, and form of dorsal pseudointerarea, the Tourmakeady valves are similar to *A. minutissima* Cooper (1956: 212), the type species of the genus from the Middle Ordovician Pratt Ferry Formation of Alabama. Some differences are discernible, however. In particular the Tourmakeady specimens are larger, much thicker shelled, and have wider dorsal pseudointerarea, but until the consistency of these differences can be confirmed or refuted in a larger sample, specific identification is withheld.

Family **PATERULIDAE** Cooper, 1956

Genus ***ELLIPTOGLOSSA*** Cooper, 1956

Elliptoglossa sp.

Fig. 23

Diagnosis. Large, thick-shelled *Elliptoglossa*, with long, low, median septum in brachial valve; dorsal limbus arched posteromedially into narrow, ventrally convex, fold.

Description. Large, elongately-oval *Elliptoglossa*, 76% as wide as long; lateral and anterior margins smoothly rounded, with slightly tapering, obtusely rounded, posterior margin; brachial valve gently convex in lateral profile, becoming less convex anteriorly; dorsal umbo swollen, beak projecting posteriorly beyond posterior margin of valve; external surfaces strongly mineralized, but concentric growth-lines are apparent here and there.

Interior of brachial valve with strongly-developed, flattened, marginal limbus up to 0·7 mm wide posteromedially but becoming less strongly developed anteriorly and anterolaterally; limbus elevated above floor of valve posteriorly and posterolaterally, and arched posteromedially into narrow, ventrally convex, fold of shell; floor of brachial valve with low median septum extending anteriorly for about 55% of valve length from beneath limbus; median septum with maximum width of 0·8 mm posteriorly, becoming narrower and slightly more elevated anteriorly; pair of arcuate transmedian (?) muscle scars, convex posteriorly and with maximum width of 0·8 mm, impressed symmetrically on either side of median septum, 2·4 mm anterior of posterior margin of valve.

FIGURED MATERIAL. Complete brachial valve, BB 95405: length 8·2 mm, width 6·2 mm. Loc. 1.

DISCUSSION. The available material consists of a single strongly mineralized brachial valve. The elongately-oval shape, strongly developed limbus and posteriorly convex muscle scars of the Irish specimen suggest a close affinity with *E. ovalis* Cooper, the type species of *Elliptoglossa*, from the Ordovician of the north-eastern U.S.A. (Cooper 1956: 242). However, the Tourmakeady specimen can readily be distinguished from *E. ovalis*, as the latter has a much shorter median septum which does not extend posteriorly of the muscle scars, and lacks a posteromedian fold in the limbus. The Tourmakeady *Elliptoglossa* differs from *E. sylvanica* Cooper, from the Ordovician of North America (Cooper 1956: 244) and the U.S.S.R. (Popov 1980: 80), in having a median septum in the brachial valve.

While the distinctive morphology of the Irish *Elliptoglossa* suggests that it represents a new species, the fact that only one specimen has been recovered precludes formal recognition.

Order **ACROTRETIDA** Kuhn, 1949

Suborder **ACROTRETINA** Kuhn, 1949

Superfamily **ACROTRETACEA** Schuchert, 1893

Family **ACROTRETIDAE** Schuchert, 1893

Subfamily **ACROTRETINAE** Schuchert, 1893

Genus *CONOTRETA* Walcott, 1889

Conotreta lepton sp. nov.

Figs 24–27

DIAGNOSIS. Minute, thin-shelled, transversely oval to subcircular *Conotreta* with moderately conical pedicle valve about three-quarters as long as wide and half as high as wide; brachial valve gently convex, about four-fifths as long as wide and one-tenth as deep as wide; dorsal median septum simple, blade-like, extending about three-fifths of valve length.

NAME. Greek, λεπτόν, a small coin.

DESCRIPTION. Minute, thin-shelled, transversely oval to subcircular *Conotreta*, translucent to pale green in colour, with smoothly and evenly rounded anterior and lateral margins and straight posterior margin; pedicle valve averaging 74% as long as wide at commissure ($\bar{l}$ mm (var l) 1·21 (0·05), $\bar{w}$ mm (var w) 1·65 (0·10), r = 0·941; n = 8) with moderately conical lateral profile averaging 47% as high as wide at posterior margin ($\overline{th}$ mm (var th) 0·78 (0·02), $\bar{w}$ mm (var w) 1·65 (0·10), r = 0·910; n = 8); external surfaces ornamented by fine concentric lamellae numbering 24 per 100 μm at 100 μm anteromedially of ventral umbo; apex of pedicle valve situated posteriorly, with prominent, conical, protegulum, circular in outline and averaging 11% as long as valve in two specimens; external surface of protegulum with evenly spaced circular pits ranging 1·6–2·4 μm in diameter; minute, circular pedicle foramen, 23 μm and 25 μm in diameter in two specimens, situated slightly posteriorly of rounded apex of protegulum, at end of short, circular pedicle tube directed obliquely posteroventrally to overhang flattened, triangular, apsacline to procline pseudointerarea which is not divided medially; interior of pedicle valve with prominent apical process as boss of shell developed along anteroventral slope of valve and forming anterior wall of transversely oval internal pedicle opening.

Brachial valve transversely elliptical in outline, averaging 80% as long as wide ($\bar{l}$ mm (var l) 1·39 (0·08), $\bar{w}$ mm (var w) 1·74 (0·13), r = 0·977; n = 7), gently and smoothly convex in lateral profile, broadly convex in anterior profile with flattened margins, and averaging 11%

as deep (th) as wide ($\bar{th}$ mm (var th) 0·16 (0·01), $\bar{w}$ mm (var w) 1·74 (0·13), $r = 0{\cdot}801$; $n = 7$); dorsal umbo rounded, triangular, beak projecting posteriorly of posterior margin of valve; interior of brachial valve with short, concave, anacline pseudointerarea separating narrowly triangular propareas; posterior margin of pseudointerarea rounded, anteriorly convex, elevated above floor of valve and medially buttressed to floor of valve by large, thickened, rounded boss of shell; floor of brachial valve with short, low, blade-like median septum extending anteriorly from median buttress in juveniles but subject to strong resorption along its posterior slope during growth and becoming separated from median buttress in adults and progressively more triangular in lateral profile; median septum (ls) extending anteriorly on average 60% of valve length ($\bar{l}$ mm (var l) 1·39 (0·08), $\bar{l}_s$ mm (var l_s) 0·83 (0·03), $r = 0.963$; $n = 7$); apex of triangular median septum situated posteriorly, rounded and thickened, and may be extended posteroventrally or anteroventrally as short, erect, cylindrical rod of shell; elongately oval to subcircular cardinal muscle scars, with dimensions of 0·4 × 0·3 mm and 0·7 × 0·6 mm in two specimens, impressed posteromedially on floor of valve symmetrically on either side of median septum and diverging anteriorly from beneath pseudointerarea at 50° with median axis of valve; anterior and anterolateral margins of muscle scars may be defined by elevated, thickened, crescentic ridges of shell.

HOLOTYPE. Complete pedicle valve, BB 95377: length 1·2 mm, width 1·4 mm. Fig. 24.

PARATYPES. Conjoined valves, BB 95419a, b (length 1·1 mm, width 1·5 mm); incomplete pedicle valve, BB 95418; brachial valve, BB 95378 (length 1·0 mm, width 1·2 mm).

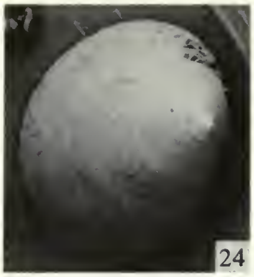
TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. Almost 30 well-preserved acrotretid valves, including conjoined pairs, which have been recovered from the Tourmakeady Limestone, are assigned to *Conotreta*. The short, simple, blade-like median septum and strong posteromedially-situated cardinal muscle scars in the brachial valve, and the moderately conical pedicle valve with a prominent apical process, are diagnostic of *Conotreta*. Several authors have commented on the fact that this genus may be a junior synonym of *Acrotreta* (e.g. Cooper 1956: 248, Biernat 1973: 67). The type material of the latter genus has been lost, however, and its internal structure is unknown; it therefore seems wiser to follow the convention adopted by other workers and assign the Tourmakeady material to *Conotreta* until such time as topotypic *Acrotreta* material can be examined.

Of published older Ordovician species of *Conotreta* from North America, *C. lepton* is close to *C. multisinuata* Cooper (1956: 253) from deposits in Virginia, Alabama and Tennessee, but can readily be distinguished because the latter species has a sulcate brachial valve, and strongly impressed mantle canals in the pedicle valve. Both *C. apicalis* Cooper (1956: 249) from the Pratt Ferry Formation of Alabama, and *C. magna* Cooper (1956: 252) from the Whitesburg Formation of Tennessee, are considerably larger than *C. lepton*, and also differ in having a much more highly conical pedicle valve. *C. apicalis monstrata* from the Ordovician of Kazakhstan (Popov 1980: 89) differs from *C. lepton* in having a much more highly conical pedicle valve, a proportionately larger median septum, and more strongly developed concentric ornamentation.

C. mica Goryanskiĭ from the Ordovician of the Russian Platform (Goryanskiĭ 1969: 64) and north-east Poland (Biernat 1973: 67) differs from *C. lepton* in having a narrower dorsal pseudointerarea with a straight anterior margin, and a proportionately longer dorsal median septum. These two criteria also serve to distinguish *C. lepton* from *C. mica*? from the Ordovician Antelope Valley Limestone of southern Nevada (Krause & Rowell 1975: 38).

When compared with the majority of described species of *Conotreta, C. lepton* stands out as being uniformly smaller and exceptionally thin-shelled. Both of these features can sometimes be considered indicative of juvenile growth stages, as indeed can the absence of mantle canal impressions. But all other internal features considered characteristic of adult *Conotreta* are readily apparent in the Tourmakeady specimens, and therefore there is no basis for assuming that the sample consists solely of juveniles.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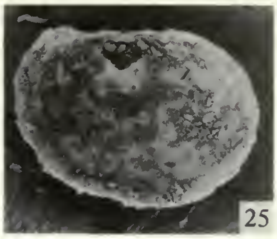
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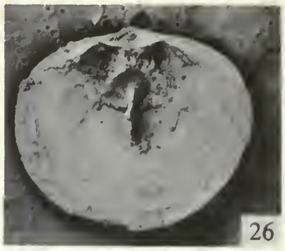
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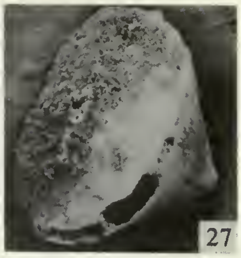
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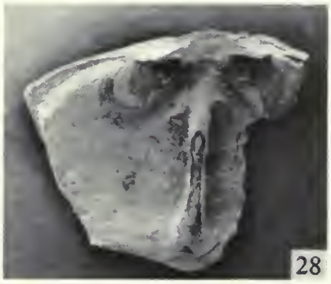
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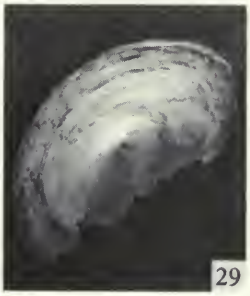
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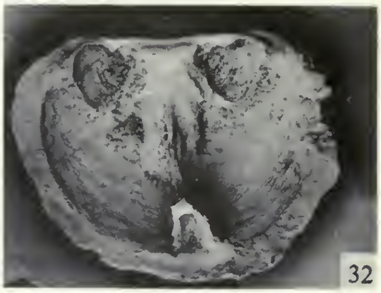
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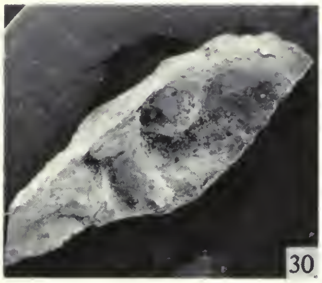
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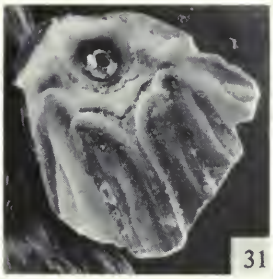
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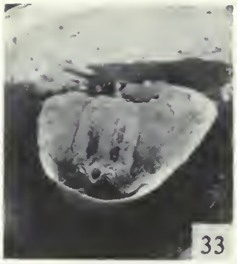
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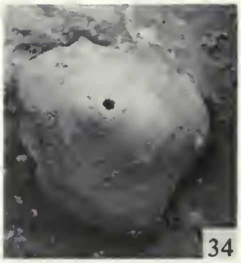
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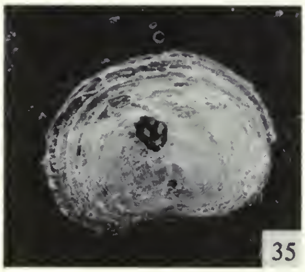
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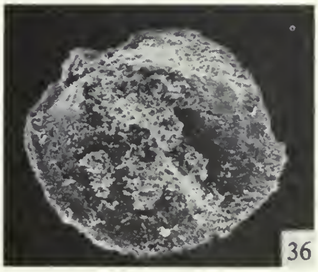
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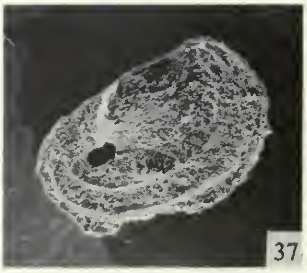
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Figs 24–27 *Conotreta lepton* sp. nov. Fig. 24, **holotype** BB 95377, exterior of pedicle valve, ×28; Fig. 25, paratype BB 95418, interior of incomplete pedicle valve, ×28; Fig. 26, paratype BB 95378, interior of brachial valve, ×28; Fig. 27, paratype BB 95419a, b, conjoined valves, ×28.

Figs 28–31 *Conotreta* sp. Fig. 28, BB 95424, interior of incomplete brachial valve, ×8; Fig. 29, BB 95425, exterior of incomplete pedicle valve, ×8; Fig. 30, BB 95426, interior of incomplete brachial valve, ×7; Fig. 31, BB 95427, interior of incomplete pedicle valve, ×18.

Figs 32–34 *Ceratreta dilatata* sp. nov. Fig. 32, **holotype** BB 95447, interior of brachial valve, ×16; Fig. 33, paratype BB 95448, interior of incomplete pedicle valve, ×11; Fig. 34, paratype BB 95449, exterior of incomplete pedicle valve, ×11.

Figs 35–37 *Scaphelasma* cf. *septatum* Cooper. Fig. 35, BB 95428, conjoined valves, ×19; Fig. 36, BB 95429, interior of brachial valve, ×31; Fig. 37, BB 95430, exterior of brachial valve, ×22.

Conotreta sp.

Figs 28–31

DIAGNOSIS. Large, thick-shelled, transversely elliptical *Conotreta* about half as long as wide; pedicle valve moderately conical with apex situated at about 50% of valve length; brachial valve gently convex, with simple blade-like median septum extending about seven-tenths of valve length.

DESCRIPTION. Large, thick-shelled, transversely elliptical *Conotreta*, estimated to have attained a maximum length and width of approximately 5 mm and 9 mm respectively, with smoothly and gently rounded anterior and posterior margins, and narrowly rounded lateral margins; external surfaces ornamented by fine concentric fila numbering 30 per mm at 1 mm anteromedially of posterior margin of brachial valve; pedicle valve narrowly conical in lateral profile, broadly conical in anterior profile, with minute, sharply tapering umbo situated at mid-point of valve; pedicle foramen minute, circular, about 0·15 mm in diameter, and situated apically; pseudointerarea of pedicle valve poorly to moderately well defined, smoothly rounded or slightly flattened, and undivided; interior of pedicle valve with strongly thickened apical process along anterior slope of valve forming anterior margin of enlarged, subcircular, pedicle tube; anterior slope of pedicle valve with strongly developed pinnate mantle canal system defined by at least six narrow, elevated, parallel-sided to subtriangular ridges, 0·1–0·2 mm wide and with a maximum height of 0·2 mm dorsomedially, radiating anteriorly and anterolaterally from apical process; branches of mantle canals averaging 0·4 mm in width (range 0·3–0·5 mm) in one specimen; pair of small, subcircular to elongately oval cardinal (?) muscle pits impressed on anterolateral margin of apical process and thickened valve floor.

Brachial valve gently convex posteromedially, becoming flattened posterolaterally; dorsal umbo rounded, low, poorly defined, extended posteriorly of posterior margin of valve for a short distance; interior of brachial valve with narrow, anacline, adnate, pseudointerarea with sunken median plate, 1·4 mm wide × 0·5 mm long in one specimen, separating poorly-defined, narrowly triangular propareas; posteromedian margin of pseudointerarea buttressed to thickened valve floor by rounded boss of shell, which may be extended anterolaterally as pair of short, rounded processes; floor of valve with low, blade-like, median septum with thickened, rounded, rod of shell developed along its posterior slope and extending anterodorsally beyond apex of median septum as rounded, erect, boss of shell; median septum estimated to have extended anteriorly for about 70% of maximum valve length, with the apex situated at about 50% of its maximum length; paired subtriangular to elongately oval cardinal muscle scars, 1·0 mm long × 0·6 mm wide in one specimen, impressed posterolaterally on elevated, thickened boss of shell strongly grooved by growth-lines, and diverging anteriorly at 60° to median axis of valve.

FIGURED MATERIAL. Incomplete pedicle valves, BB 95425 (width 4·0 mm), 95427; incomplete brachial valves, BB 95424, 95426. Loc. 1.

DISCUSSION. Although fragmentary, it is clear that the Tourmakeady fauna included one of the largest representatives of *Conotreta* yet described, matched in size only by *C. gigantea* Cooper (1956: 251), from the Pratt Ferry Formation of Alabama, and *C. magna* Cooper (1956: 252), from the Whitesburg Formation of Tennessee. The two American species can readily be distinguished from the Tourmakeady specimens, however, as both have a narrowly conical pedicle valve with a posteriorly situated apex, and a well-defined, medially divided, ventral pseudointerarea. The strongly transversely-oval outline also serves to distinguish the Irish material from the circular to slightly transversely-oval American species.

C. apicalis monstrata Popov (1980: 88), from the Ordovician of Kazakhstan, differs from the Irish specimens in having a much wider dorsal pseudointerarea, an almost straight posterior margin, and stronger external ornamentation. However, although the Irish specimens are distinctive, specific recognition has been withheld in view of the sparseness of the available sample.

Subfamily **CERATRETINAE** Rowell, 1965

Genus ***CERATRETA*** Bell, 1941

Ceratreta dilatata sp. nov.

Figs 32–34

DIAGNOSIS. Transversely oval *Ceratreta*, about four-fifths as long as wide; brachial valve interior with long, low, median septum bifurcating anteriorly to form arch-like process and flanked posteriorly by broad, low, flattened platform.

NAME. 'Swollen'.

DESCRIPTION. Medium-sized, transversely oval *Ceratreta*, 85% as long as wide in one specimen, with strongly rounded lateral and anterior margins and almost straight posterior margin; external surfaces ornamented by fine concentric fila numbering 18 per mm in the median region of the brachial valve.

Pedicle valve strongly conical in lateral profile, with sharply tapering, rounded apex situated posteriorly of posterior margin of valve; ventral pseudointerarea procline, flattened, triangular, subdivided medially by faint, broad intertrough; pedicle foramen minute, elongately oval, 0·1 mm long × 0·05 mm wide in one specimen, situated posteriorly of apex along posterior slope of valve.

Interior of pedicle valve with well-developed apical process as swollen boss, extended medially along inner wall of ventral pseudointerarea as rounded, elevated ridge bounding circular internal pedicle opening; two narrow branches of baculate mantle canal system impressed symmetrically on either side of apical process along inner wall of ventral pseudointerarea.

Brachial valve gently convex in lateral profile, with prominent rounded umbo extending posteriorly beyond posterior margin of valve; brachial valve interior with well-defined, concave, apsacline, triangular pseudointerarea, undivided medially, and with a straight anterior margin buttressed medially to floor of valve by broad, thickened, boss of shell; floor of brachial valve with long, low, thickened median septum extending almost to flattened anterior margin of valve; anterior margin of median septum elevated medially and bifurcating to form narrow, incurved, anterolateral lobes disposed as an arch-like process; median septum flanked posteriorly by broad, low, thickened, platform extending for about half of valve length; strong, subtriangular cardinal muscle scars, measuring 0·5 mm × 0·4 mm in one specimen, impressed posterolaterally on valve floor, and diverging anteriorly at 60° to median axis of valve.

HOLOTYPE. Complete brachial valve, BB 95447: length 2·2 mm, width 2·6 mm. Fig. 32.

PARATYPES. Incomplete pedicle valves, BB 95448, 95449.

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. The Tourmakeady specimens are undoubtedly representatives of the rare acrotretid genus *Ceratreta*, which is known primarily from Upper Cambrian deposits in the U.S.A. (Bell 1941). Features such as an elongate apical process in the pedicle valve, a well-developed undivided dorsal pseudointerarea, and a long dorsal median septum elevated anteriorly, are diagnostic of this genus.

C. dilatata is readily distinguished from *C. hebes*, the type species of the genus from the Upper Cambrian of North America (Bell 1941: 233), as the latter has a bluntly conical pedicle valve, and lacks anterolateral lobes on the dorsal median septum. In addition, the flattened platform flanking the median septum is unique to *C. dilatata*.

Subfamily **SCAPHELASMATINAE** Rowell, 1966

Genus ***SCAPHELASMA*** Cooper, 1956

Scaphelasma cf. ***septatum*** Cooper

Figs 35–37

cf. 1956 *Scaphelasma septatum* Cooper: 260.

The etched residues of the Tourmakeady Limestone, recovered from Loc. 1, contained a small number of minute, well-preserved, complete valves, which are undoubtedly representatives of the distinctive acrotretid genus *Scaphelasma*. The specimens, one conjoined pair (BB 95428) and three brachial valves (BB 95429–30, BB 95517), are transversely oval in outline, averaging 76% (range 69–86%) as long as wide in 3 specimens, with smoothly rounded anterior and lateral margins and a straight posterior margin. The valves are ornamented by concentric growth-lines which become strongly lamellose peripherally. The pedicle valve is moderately conical in lateral profile being 46% as high as wide, and has a strongly rounded, posteriorly situated, umbo. The narrowly triangular, procline ventral pseudointerarea is subdivided medially by a well-developed intertrough which is very narrow ventrally but becomes wider dorsally. The brachial valve is convex posteromedially, with a prominent, rounded umbo projecting posteriorly of the posterior margin of the valve. The margins of the brachial valve are flattened or slightly concave. On the interior of the brachial valve the dorsal pseudointerarea is narrow and undivided. A short, triangular, median septum arises at about the midpoint of the valve and extends anteriorly almost to the anterior margin of the valve.

A comparison between the Tourmakeady specimens and *S. septatum* Cooper (1956: 260), the type species of *Scaphelasma* from the Middle Ordovician Pratt Ferry formation of Alabama, indicates that no valid morphological criteria exist to justify the erection of a new species. The size and proportions of valves from the Irish and American localities are very similar. Thus, the holotype of *S. septatum*, a pedicle valve, is 78% as long as wide and 43% as high as wide, while the comparable proportions for the sole pedicle valve (BB 95428) in the Tourmakeady sample are 69% and 46% respectively. Some slight differences were detected, however; notably fewer concentric lamellae and a proportionately wider ventral pseudointerarea on the Tourmakeady specimen. In addition, the characteristic pattern of large and small pits on the protegular surface are consistently larger in the Irish valves, averaging 3·85 μm (range 3·6–4·2 μm) and 430 nm (range 300–500 nm) for larger and smaller pits respectively, as compared with a maximum of 3·0 μm and 300 nm recorded by Biernat & Williams (1970: 494) for topotypic *S. septatum*.

Subfamily **TORYNELASMATINAE** Rowell, 1966

Genus ***MYLLOCONOTRETA*** nov.

Diagnosis. Small, transversely to elongately oval acrotretid, with juvenile pedicle and brachial valves moderately conical and gently convex or plane respectively, adult valves strongly geniculate anteriorly and anterolaterally; external surfaces ornamented by fine concentric fila which are wavy, discontinuous, narrowly tapering distally and occasionally nodose during early growth stages, but becoming evenly-spaced and smoothly rounded distally on post-geniculation valve surfaces.

Pedicle valve with minute, transversely oval, smooth protegulum, ventral pseudointerarea broadly triangular, procline, and undivided.

Brachial valve with narrow, anacline, undivided pseudointerarea; median septum large, blade-like, extending to anterior margin of valve and surmounted by concave, bilobed, plate; strong, elevated, cardinal muscle platforms developed posterolaterally on valve floor.

Name. Greek, *μυλλός*, crooked.

Type species. *Mylloconotreta elimata* sp. nov., from the Tourmakeady Limestone, Co. Mayo.

Discussion. The conical pedicle valve with its minute apical foramen and the strong dorsal median septum are features which immediately establish the new genus as a repesentative of the Acrotretidae. Furthermore, its inclusion within the Torynelasmatinae is equally justifiable, as the concave surmounting plate on the dorsal median septum is diagnostic of that subfamily.

The strong geniculation in both valves associated with the change in external ornamentation are features which have not previously been recorded in any torynelasmatinid, and therefore serve to distinguish *Mylloconotreta* from other genera assigned to this small subfamily. Apart from lacking geniculation, *Torynelasma* Cooper also differs in having an apsacline rather than a procline ventral pseudointerarea and a strongly conical protegulum, usually with well-developed external pitting. The taxonomic significance of this latter feature has not been established, but the additional difference in the shape of the ventral protegulum indicates differences in growth during early life.

The new genus is known at present only from the Tourmakeady Limestone.

Mylloconotreta elimata sp. nov.

Figs 38–44

Diagnosis. Small, moderately to strongly transversely oval *Mylloconotreta*, averaging seven-tenths as long as wide, with straight posterior margin, strongly rounded lateral margins, and smoothly and gently rounded anterior margins; external surfaces ornamented by fine concentric fila numbering about 15 per 100 μm at 1 mm anteriorly of ventral umbo; interior of brachial valve with strong triangular median septum surmounted by concave, heart-shaped plate.

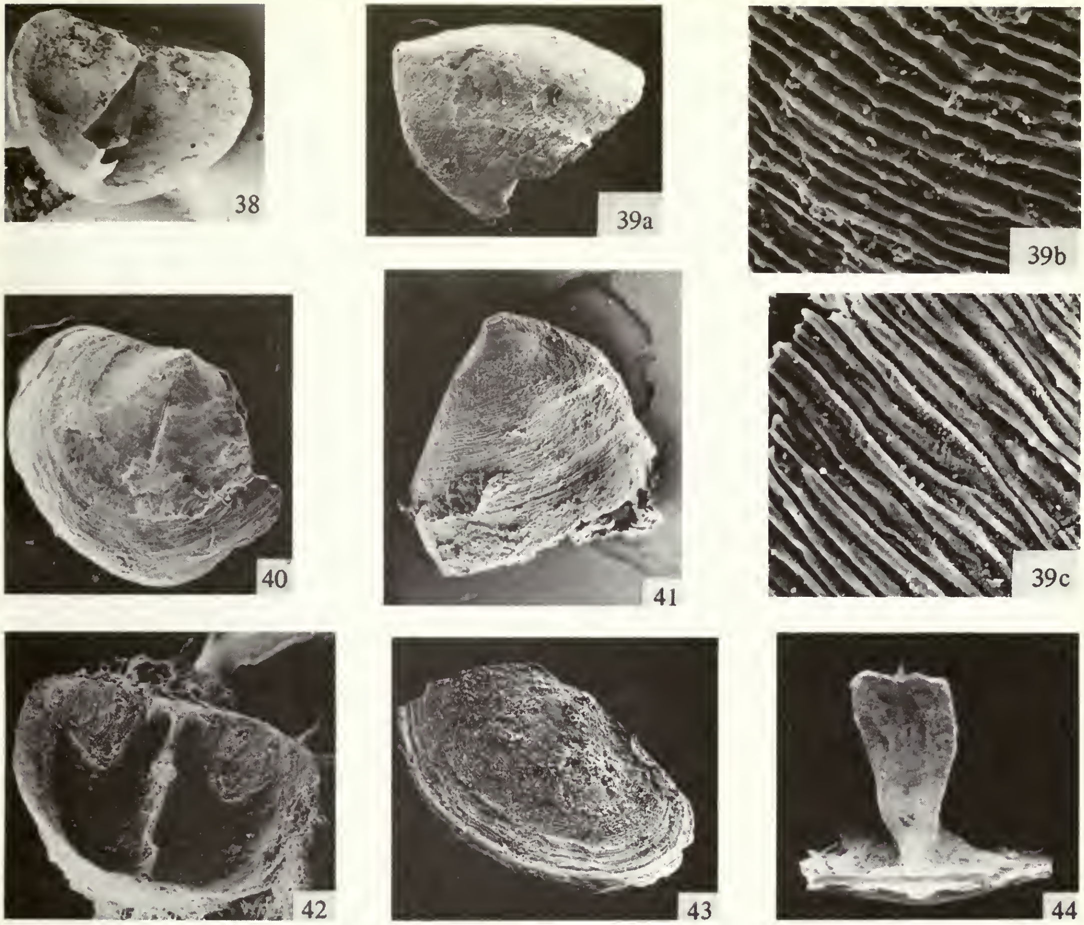
Name. 'Made smooth'.

Description. Small, moderately to strongly transversely oval *Mylloconotreta*, on average 69% as long as wide ($\bar{l}$ mm (var l) 1·19 (0·06), $\bar{w}$ mm (var w) 1·71 (0·07), $r = 0{\cdot}815$; $n = 7$ brachial valves) with straight posterior margin, strongly rounded lateral margins, and smoothly and gently rounded anterior margins; external surfaces ornamented by fine concentric fila with wavelength and amplitude averaging 7 μm and 4 μm respectively over the entire valve surface; fila discontinuously developed, irregularly undulating, wavy, and narrowly tapering distally on juvenile valve surfaces, but changing abruptly at zone of geniculation to become evenly spaced, and smoothly rounded on post-geniculation valve surfaces.

Pedicle valve moderately conical in lateral profile, with strong geniculation along lateral and anterolateral margins, developed at an average distance of 0·6 mm (range 0·4–0·7mm in 5 specimens) from ventral apex along anterior slope of valve; geniculate zone directed dorsally so that adult valve appears as a parallel-sided, cylindrical tube distally, surmounted proximally by triangular juvenile cone; ventral beak situated slightly posteriorly of mid-point of valve; pedicle foramen minute, circular, with a diameter of about 140 × 110 μm in one specimen; external surfaces of protegulum smooth; ventral pseudointerarea broadly triangular, procline, flattened, and undivided.

Brachial valve gently convex to plane in lateral profile when juvenile, becoming strongly and sharply geniculate anteriorly and anterolaterally in later growth stages, with a maximum thickness anteromedially of up to 67% of valve length (average 45%; range 23–67% in 6 specimens); angle of geniculation variable, ranging from 30° to more than 90°; external surfaces of brachial valves with variably-developed median sulcus, very narrow in juveniles, becoming broader and moderately rounded anteriorly.

Dorsal interior with narrow, anacline undivided pseudointerarea, sunken medially, elevated along its anterior margin, and buttressed medially to floor of valve by T-shaped boss of shell; floor of valve with large, blade-like, triangular median septum arising just forward of pseudointerarea and extending to anterior margin of valve in all growth stages; posterior slope of median septum with erect, concave, surmounting plate, very narrow dorsally but



Figs 38–44 *Mylloconotreta elimata* gen. et sp. nov. Fig. 38, **holotype** BB 95420, interior of brachial valve, ×16; Fig. 39a, b, c, paratype BB 95421: a, exterior of incomplete pedicle valve, ×21; b, c details of ornamentation, both ×200; Fig. 40, paratype BB 95422, oblique view of exterior of incomplete brachial valve, ×24; Fig. 41, paratype BB 95423, lateral view of exterior of incomplete pedicle valve, ×14; Fig. 42, paratype BB 95355, interior of brachial valve, ×14; Fig. 43, paratype BB 95354, oblique view of exterior of incomplete brachial valve, ×25; Fig. 44, paratype BB 95357, posterior view of incomplete brachial valve, ×31.

widening progressively ventrally and extending beyond ventral apex of median septum as pair of symmetrically-disposed, rounded lobes reaching 81% and 78% as high as valve length in two specimens; strong, elevated, cardinal muscle platforms, triangular to tear-shaped in outline and averaging 73% as long as wide ($\bar{l}_{sc}$ mm (var l) 0·40 (0·006), $\bar{w}_{sc}$ mm (var w) 0·29 (0·001), $r = 0.789$; $n = 7$), developed posterolaterally on floor of valve and diverging anteriorly at 40–50° with median axis of valve.

HOLOTYPE. Brachial valve, BB 95420: length 1·6 mm, width 2·1 mm. Fig. 38.

PARATYPES. Incomplete pedicle valves, BB 95421, 95423, 95354 (length 1·0 mm); brachial valve, BB 95355 (length 1·2 mm, width 1·6 mm); incomplete brachial valves, BB 95422 (length 1·3 mm), 95357.

TYPE HORIZON AND LOCALITY. Loc. 1.

Mylloconotreta sp.

Figs 45–46

Specimens assigned to *Mylloconotreta elimata*, above, show the sort of variation expected of a morphologically homogeneous species. However, the Tourmakeady residues have also yielded a small number of congeneric valves which may be a separate stock. These valves (BB 95431–95434) are immediately distinguishable in being strongly elongately oval, although in the nature of the ornamentation and form of dorsal median septum they are similar to *Mylloconotreta*. The sample is too small to preclude attribution of differences in outline to sexual dimorphism, distortion, or even an indication of high intraspecific variability. Among these elongately oval specimens are a few strongly geniculate pedicle valves which certainly belong to the new genus, although none of the matching brachial valves shows the strong geniculation which would be expected in similarly-sized specimens of *M. elimata*. A close examination of the anteromedian margin of these brachial valves does reveal a slight ventrally-directed deflection in the growth direction, which may indicate incipient geniculation. In all probability, therefore, these valves are not fully mature.

The taxonomic status of these elongately oval shells can only be resolved when a much larger sample is available for study; until more material has been obtained, specific identification is withheld.

? Superfamily **ACROTRETACEA** Schuchert, 1893

Family **EOCONULIDAE** Rowell, 1965

Genus ***EOCONULUS*** Cooper, 1956

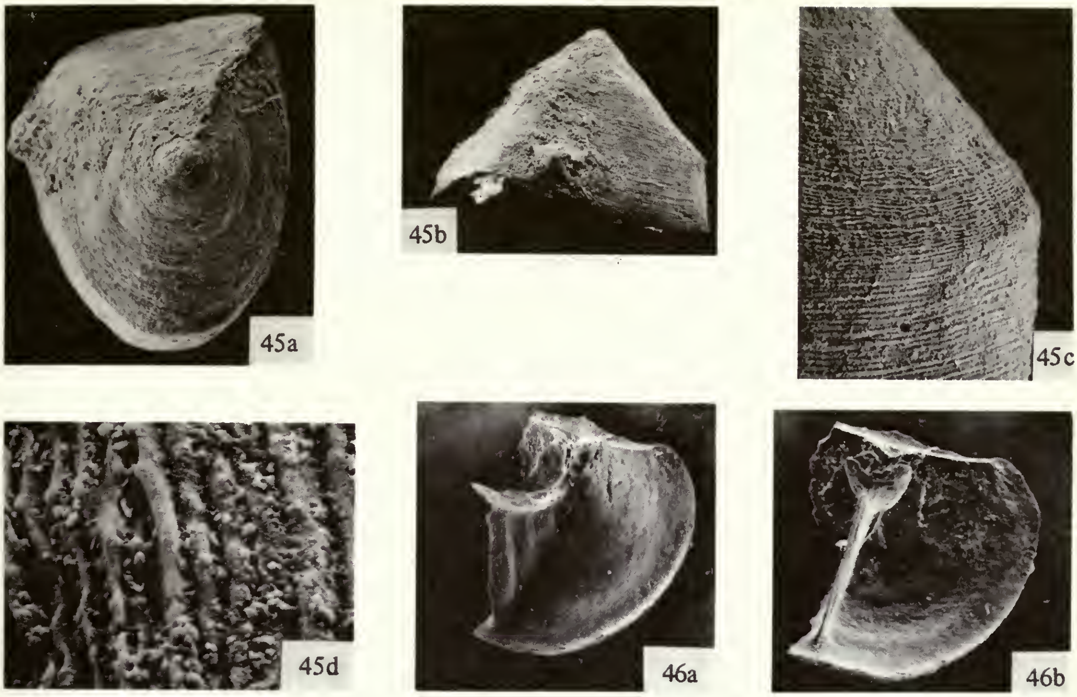
Eoconulus sp.

Fig. 47

The etched residues of Tourmakeady Limestone exposed at Loc. 1 yielded a single example of the enigmatic genus *Eoconulus*. The specimen (BB 95440), which is thought to be an incomplete pedicle valve, is subquadrate in outline, and is estimated to have been 0·8 mm long and 1·0 mm wide when complete. In lateral profile the valve is an imperfect cone, with a large, flattened, subcircular apex situated posteriorly. The external surface is ornamented by fine discontinuous fila numbering about 15 per mm over the anterior slope of the valve. Internally a prominent, rounded process is developed at the posteromedian margin of a thickened apical region. The median process is flanked by relatively large, deep, pits.

Eoconulus is an unusual genus, and when first described was known only from its brachial valve (Cooper 1956: 282). Subsequently, however, Krause & Rowell (1975: 64) recovered conjoined pedicle and brachial valves from the Lower Ordovician Antelope Valley Limestone of southern Nevada. Prior to this discovery it had been assumed that *Eoconulus* lived attached to the substrate by a pedicle valve which was not preserved because it was unmineralized. Having recovered mineralized pedicle valves with prominent attachment scars, Krause & Rowell emended the diagnosis of the genus to read 'cemented by a pedicle valve which may or may not be mineralised'. The work of Krause & Rowell on the Nevada species indicates that the pedicle and brachial valves of *Eoconulus* are externally similar, both being moderately conical in lateral profile. Internally, however, they are readily distinguishable, as the pedicle valve has a prominent apical process. If this feature is assumed to be characteristic, then the prominent internal process in the Tourmakeady specimen immediately identifies it as a pedicle valve. With only a single, incomplete, specimen available for study a detailed comparison with previously described species of *Eoconulus* is clearly impracticable. However, it is interesting that the sole representative of the genus in the Tourmakeady fauna appears to be a pedicle valve; most commonly only brachial valves are recovered (Cooper 1956: 282, Biernat 1973: 111).

The taxonomic affinities of *Eoconulus* are problematical. Originally it was decided that the



Figs 45–46 *Mylloconotreta* sp. Fig. 45a, b, c, d, BB 95431, pedicle valve: a, ventral view, ×22; b, lateral view, ×17; c, enlarged lateral view, ×54; d, ornamentation, ×420. Fig. 46a, b, BB 95432, incomplete brachial valve: a, oblique lateral view; b, anterior view; both ×25.

genus was most appropriately incorporated within the Craniacea because of its attached mode of life (Cooper 1956: 282). The subsequent discovery of a mineralized conical pedicle valve with a prominent apical process led Krause & Rowell to assign *Eoconulus* to the Acrotretacea, albeit tentatively. Biernat (1963: 111) had also considered this latter possibility, but had rejected it because the pattern of protegular pits seen on *Eoconulus* differs from that seen on most acrotretaceans (Biernat & Williams 1970: 499). However, the taxonomic significance of differences in protegular surface sculpture has not been ascertained, and pits are indeed absent from some undoubted acrotretaceans, such as *Mylloconotreta* gen. nov. from the Tourmakeady Limestone (p. 203). Therefore, it seems more appropriate to follow the procedure adopted by Krause & Rowell, while acknowledging that the genus is at best only tentatively assigned to the Acrotretacea.

Superfamily **DISCINACEA** Gray, 1840

Family **DISCINIDAE** Gray, 1840

Subfamily **ORBICULOIDEINAE** Schuchert & LeVene, 1929

Genus ***SCHIZOTRETA*** Kutorga, 1848

Schizotreta sp.

Figs 48–49

The residues from the Tourmakeady Limestone exposed at Loc. 1 contained one almost complete brachial valve (BB 95408), and several similarly-ornamented fragments (BB

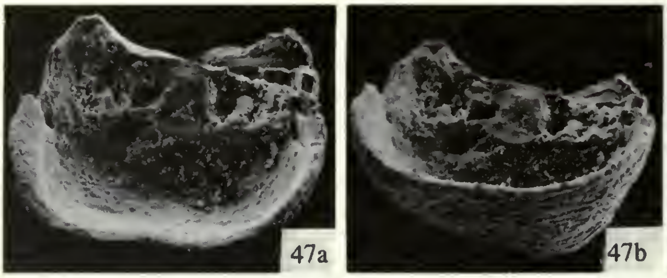
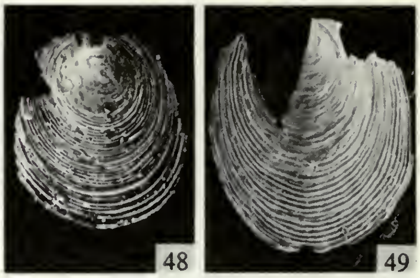


Fig. 47a, b *Eoconulus* sp. BB 95440, interior and oblique anterior views of incomplete pedicle valve, both ×42.



Figs 48–49 *Schizotreta* sp. Fig. 48, BB 95408, exterior of brachial valve, ×9; Fig. 49, BB 95518, exterior of incomplete brachial(?) valve, ×11.

95518), attributable to *Schizotreta*, especially on account of its submarginal beak (Krause & Rowell 1975: 69). A reconstruction indicates that the brachial valve was about 3 mm long and 2·5 mm wide when complete, and was elongately oval in outline with strongly and smoothly rounded anterior and lateral margins. The valve has a low conical lateral profile, 14% as high as long, with the apex situated about 0·5 mm anterior of the posterior margin. Anteriorly and anterolaterally the valve becomes almost flat. The external surfaces of all specimens are ornamented by fine, elevated, evenly-spaced, concentric fila numbering 16 per mm about 1 mm anterior of the beak. The rounded, submarginal beak of the brachial valve is separated from the posterior margin of the valve by a low, broadly triangular, hypercline pseudointerarea.

In shape and form of external ornamentation the Tourmakeady specimens are similar to congeneric species recovered from Lower and Middle Ordovician sediments from North America (Cooper 1956: 277; Krause & Rowell 1975: 69). The majority of American specimens are, however, considerably larger than the Irish ones, which are very thin-shelled and may well be juveniles. Even so, *Schizotreta* sp. from the Antelope Valley Limestone (Krause & Rowell 1975: 69) does have dimensions similar to those of the Irish specimens, although the latter are readily distinguishable in having finer and more numerous concentric fila. The inadequate sample available for study makes detailed comparisons with other described *Schizotreta* unprofitable, and specific identification impossible.

Superfamily **SIPHONOTRETACEA** Kutorga, 1848

Family **SIPHONOTRETIDAE** Kutorga, 1848

Genus ***CYRBASIOTRETA*** nov.

Diagnosis. Transversely oval siphonotretacean with conical pedicle valve and gently convex sulcate brachial valve, ornamented by increasingly strong lamellae each bearing a single row of fine, evenly-spaced, hollow spines; oval pedicle foramen tapering sharply posteriorly to small, triangular beak projecting posteriorly over large, procline, ventral pseudointerarea divided medially by faint median ridge forming pedicle trail; posterior margin of pedicle foramen closed by small concave plate; brachial valve with narrow, undivided pseudointerarea.

Name. Greek, *ϰυρβᾰσία*, a Persian hat.

Type species. *Cyrbasiotreta cirrata* sp. nov., from the Tourmakeady Limestone, Co. Mayo.

Discussion. The most distinctive feature of the new genus is its strongly conical pedicle valve, which has not been recorded previously in any siphonotretacean genus. Yet there is no doubt that *Cyrbasiotreta* is most appropriately assigned to the Siphonotretacea, as is indicated by other basic features like its hollow external spines, the well-developed pedicle trail and rudimentary dorsal pseudointerarea. Indeed the brachial valve of *Cyrbasiotreta* could, at first sight, be confused with that of *Schizambon* Walcott or *Multispinula* Rowell. *Cyrbasiotreta* can readily be distinguished from the former, however, which has a gently convex pedicle valve with a marginal beak. *Schizambon* also lacks a well-developed ventral pseudointerarea and has irregularly-distributed spines, while the plate closing the posterior margin of the pedicle foramen is adnate with the posterior margin of the valve.

The ventral pseudointerarea of *Multispinula* is much narrower than that of *Cyrbasiotreta*, and the pedicle foramen is proportionately much larger. Internally the two genera differ markedly in that the pedicle of *Multispinula* was encased within a tube.

In addition to its distinctive conical pedicle valve, there are other morphological features of *Cyrbasiotreta* which serve to distinguish it from other siphonotretacean genera. The nature of its external ornamentation and the form of the pedicle foramen are especially useful. These two features, for example, distinguish *Cyrbasiotreta* from *Karnotreta* (p. 211), the other new siphonotretacean genus from Tourmakeady, which has spines formed by the folding of lamellae and a pedicle tube ankylosed posteromedially with the inner wall of the ventral pseudointerarea. Indeed the absence of a pedicle tube internally excludes *Cyrbasiotreta* from the newly-erected subfamily Schizamboninae Havlíček (1982). *Siphonotreta* de Verneuil differs in having a well-developed pedicle tube and a strongly apsacline ventral pseudointerarea, and in being sparsely and irregularly spinose. *Helmersenia* Pander, with its sealed pedicle foramen in adult valves, can also be readily distinguished from *Cyrbasiotreta*, as can *Dysoristus* Bell which lacks external spines, and *Alichova* Goryanskiĭ which bears scattered branching spines.

The morphology of *Cyrbasiotreta* is of interest in the context of the evolutionary history of the Siphonotretacea. The origins of the group are not known with certainty, but it has been suggested, on the basis of a similarity in the structure of the dorsal posterior margin, that the acrotretaceans provided the ancestral stock (Rowell 1962: 151). Clearly the discovery of a new siphonotretacean with an acrotretacean-like pedicle valve would tend to support this view.

The new genus is at present monospecific and is known only from the small sample of predominantly incomplete specimens recovered from the Tourmakeady Limestone.

Cyrbasiotreta cirrata sp. nov.

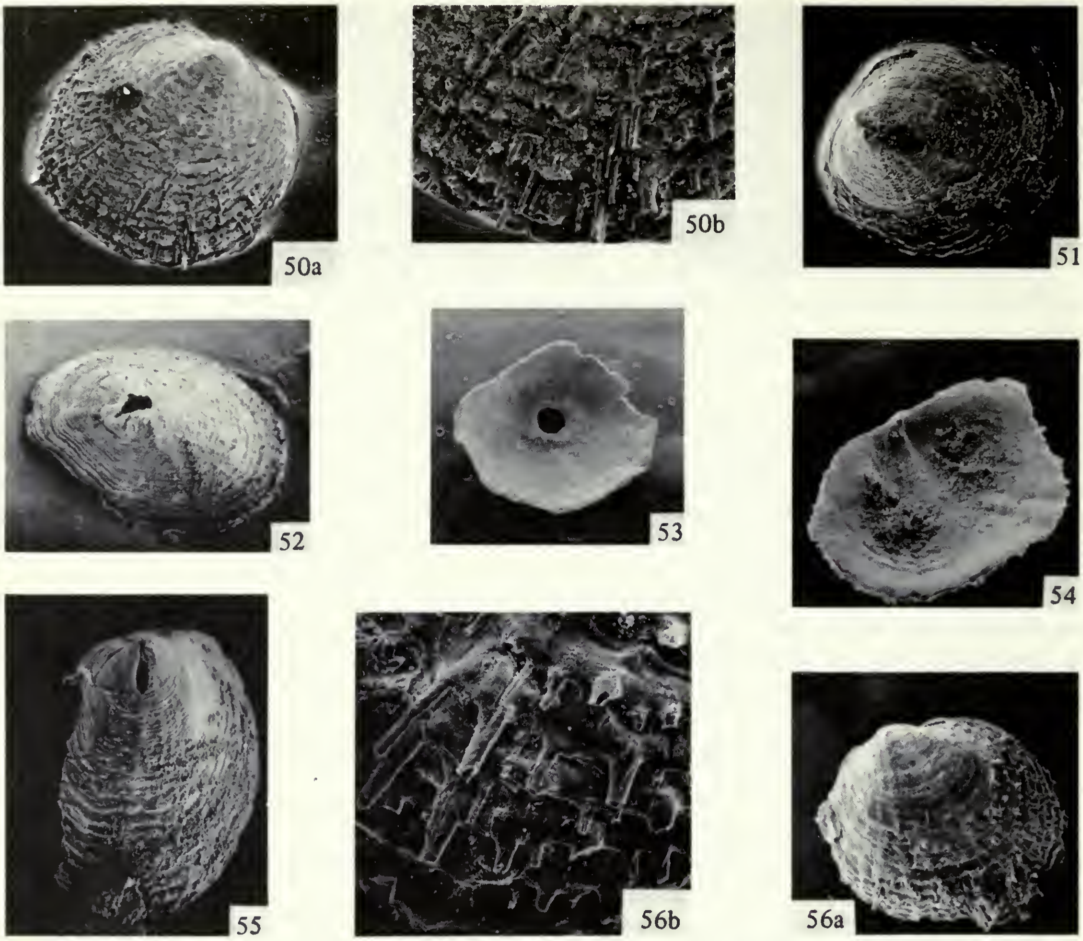
Figs 50–56

DIAGNOSIS. Small, moderately to strongly transversely oval *Cyrbasiotreta*, between three-fifths to nine-tenths as long as wide, with conical pedicle valve about three-fifths as high as long; pedicle foramen elongately oval, about two-fifths as wide as long and about one-sixth as long as valve; external surfaces ornamented by hollow, circular spines ranging up to 50 μm in diameter.

NAME. 'Fringed'.

DESCRIPTION. Small, moderately to strongly transversely oval *Cyrbasiotreta*, ranging from 60% to 90% as long as wide in 4 specimens, with smoothly rounded lateral and anterior margins and almost straight posterior margin; external surfaces becoming strongly lamellose distally with each lamella bearing single row of hollow, suberect, circular, spines along anterior margin; spines with diameters ranging 10–50 μm, and spaced at average distance of 85 μm (range 30–125 μm).

Pedicle valve conical in lateral profile, 61% as high as long in one specimen, with rounded umbo situated slightly posteriorly of mid-point of valve; pedicle foramen elongately oval, averaging 43% (range 40–48%) as wide as long in 6 specimens and 17% as long as valve in one specimen, smoothly rounded anteriorly and with rounded lateral margins tapering posteriorly to small, triangular beak projecting posteriorly to overhang well-developed, triangular, flattened, procline, ventral pseudointerarea divided medially by faint ridge; posterior margin of pedicle foramen closed by small concave plate which projects through



Figs 50–56 *Cyrbasiotreta cirrata* gen. et sp. nov. Fig. 50a, b, **holotype** BB 95436, exterior of brachial valve: a, ×16; b, enlargement of ornamentation, ×50; Fig. 51, paratype BB 95435, exterior of incomplete pedicle valve, ×20; Fig. 52, paratype BB 95437, oblique external view of distorted pedicle valve, ×14; Fig. 53, paratype BB 95439, interior of incomplete pedicle valve, ×18; Fig. 54, paratype BB 95438, interior of incomplete brachial valve, ×17; Fig. 55, paratype BB 95607, exterior of distorted pedicle valve, ×17; Fig. 56a, b, paratype BB 95608, exterior of brachial valve: a, ×15; b, enlargement of ornamentation, ×75.

umbo to form slightly elevated posterior margin of internal pedicle opening; lateral and anterior margins of internal pedicle opening thickened in some specimens to form low rounded or flattened ridge.

Brachial valve moderately convex in lateral profile with small rounded umbo projecting slightly posteriorly beyond posterior margin of valve; dorsal median sulcus very narrow posteriorly but becoming broader and shallower anteriorly; dorsal pseudointerarea very narrow, slightly sunken medially and buttressed by narrow median boss of shell in some specimens; muscle scars unknown.

HOLOTYPE. Brachial valve, BB 95436: length 2·0 mm, width 2·2 mm. Fig. 50.

PARATYPES. Incomplete pedicle valves, BB 95435, 93439, 95607; distorted pedicle valve, BB 95437; incomplete brachial valves, BB 95438, 95608 (length 2·0 mm).

TYPE HORIZON AND LOCALITY. Loc. 1.

Subfamily **SCHIZAMBONINAE** Havlíček, 1982

Genus ***KARNOTRETA*** nov.

Diagnosis. Small, subcircular, ventribiconvex siphonotretid, with truncated posterior margins; external shell surfaces ornamented by fine concentric growth-lines becoming lamellose peripherally and bearing regular rows of flattened, hollow, prone spines; pedicle valve low, conical in lateral profile with subcircular pedicle foramen situated posteriorly; ventral pseudointerarea narrow, triangular, apsacline, divided medially by low, rounded ridge.

Ventral interior with circular, dorsally-directed pedicle tube, adnate posteromedially with inner surface of ventral pseudointerarea.

Dorsal interior with narrow, thickened, anacline pseudointerarea arched medially to form convex fold of shell; floor of valve with low median septum and elongately-oval posterolateral muscle scars diverging anteriorly.

Name. Greek, *ϰάϱνον*, a horn.

Type species. *Karnotreta adnata* sp. nov., from the Tourmakeady Limestone, Co. Mayo.

Discussion. The new genus is represented by a small number of well-preserved specimens including complete pedicle and brachial valves. The taxonomic affinities of *Karnotreta* are not in doubt, as the combination of a low conical pedicle valve with a circular pedicle foramen extended into the valve interior as a tube, and the spinose external surfaces, are characteristic of the siphonotretids. Indeed, when compared with other genera at present assigned to the family, it is apparent that the features which characterize *Karnotreta* have been recorded previously, but it is their appearance in a single taxon which justifies the erection of a new genus. Thus *Multispinula* Rowell, its closest morphological comparison, resembles *Karnotreta* in having regularly-arranged rows of spines and a pedicle tube, but differs in that the spines are circular and the pedicle tube is directed anterodorsally and is not adnate with the inner wall of the ventral pseudointerarea. *Multispinula* is, in addition, much larger than *Karnotreta*, as is *Siphonotreta* de Verneuil, which can be further distinguished on the basis of a wide, strongly apsacline, ventral pseudointerarea and a proportionately smaller pedicle foramen extending through a greatly thickened ventral umbo.

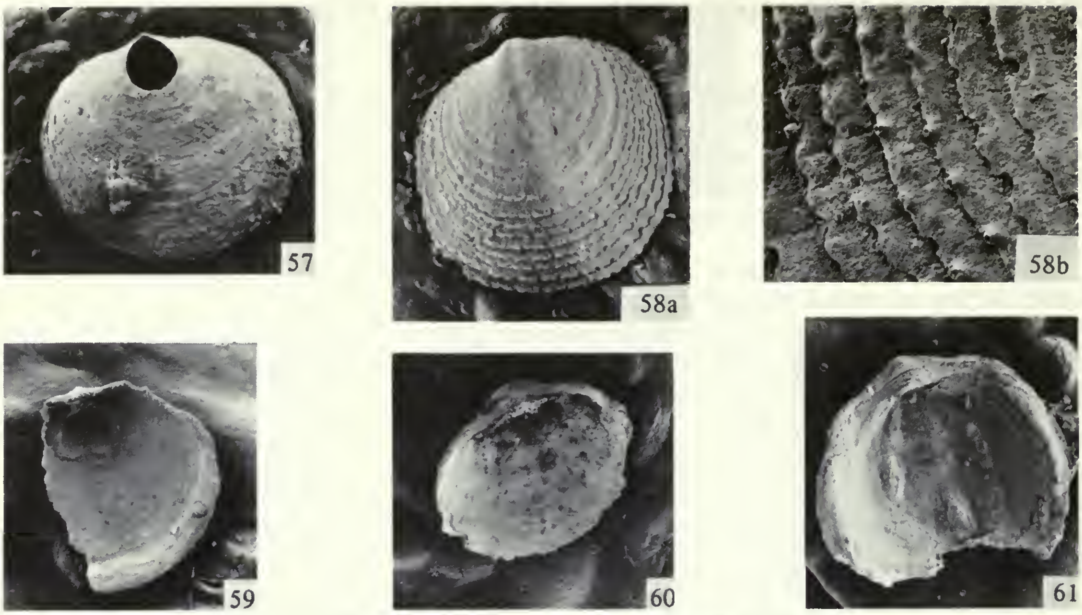
Schizambon Walcott differs from *Karnotreta* in lacking a well-developed ventral pseudointerarea, and in having external valve surfaces covered with fine spines. *Dysoristus* Bell can immediately be distinguished from the new genus as it lacks spines, and has an internal pedicle tube free of the ventral pseudointerarea. Similarly, *Helmersenia* Pander would not readily be confused with the new genus, as it has a narrow ventral pseudointerarea and scattered external spines. Differences in shell shape and ornamentation, and in the form of the brachial pseudointerarea, are the primary features distinguishing between *Karnotreta* and the poorly-known genus *Alichova* Goryanskiĭ. The latter differs at least in having distinctive, widely-spaced, erect, branching spines, a narrower dorsal pseudointerarea, and an elongately-oval shape.

At present *Karnotreta* is monospecific, and known only from the Tourmakeady Limestone. However, the form of the external spines on the new genus is distinctive; it is possible that a re-examination of previously unidentifiable spinose valves from Ordovician or Upper Cambrian successions will show *Karnotreta* to have been more widespread.

Karnotreta adnata sp. nov.

Figs 57–61

Diagnosis. Thin-shelled, subcircular, *Karnotreta*, about nine-tenths as long as wide; pedicle valve low, conical, about one-third as high as long; brachial valve interior with low, rounded, median septum and two lateral ridges; pair of elongately-oval muscle scars faintly impressed posterolaterally.



Figs 57–61 *Karnotreta adnata* gen. et sp. nov. Fig. 57, **holotype** BB 95414, exterior of pedicle valve, ×9; Fig. 58a, b, paratype BB 95415, exterior of brachial valve: a, ×9; b, enlargement of ornamentation, ×36. Fig. 59, paratype BB 95416, interior of incomplete brachial valve, ×9; Fig. 60, paratype BB 95606, interior of brachial vave, ×8; Fig. 61, paratype BB 95417, interior of incomplete brachial valve, ×9.

NAME. 'Attached'.

DESCRIPTION. Small, subcircular, ventribiconvex *Karnotreta*, on average 86% as long as wide, with evenly rounded anterior and lateral margins and truncated, rectimarginate, posterior margin; external surfaces ornamented by fine concentric growth-lines becoming lamellose peripherally and bearing rows of fine, transversely oval to subtriangular, hollow, prone spines with dimensions of up to $80 \times 35 \mu m$; pedicle valve low, conical in lateral profile, about one-third as high as long, with posteriorly-situated apex; pedicle foramen apical, subcircular, about 80% as wide as long with smoothly rounded anterior and lateral margins tapering slightly posteriorly; ventral beak small, triangular, projecting posteriorly to overhang narrow, broadly triangular, apsacline pseudointerarea divided medially by well-developed, rounded median ridge; propareas narrow, triangular, marked by growth-lines becoming lamellose and spinose dorsally; posterior margin of pedicle foramen with vertical plate projecting dorsally through umbo to form posterior margin of circular pedicle tube on valve interior; posterior margin of pedicle tube adnate medially with inner surface of ventral pseudointerarea, but becoming free posterolaterally; inner surfaces of pedicle tube finely grooved by concentric growth-lines.

Brachial valve gently convex, with faint, triangular, median sulcus, very narrow posteriorly but becoming wider and shallower anteriorly; dorsal umbo small, rounded with triangular beak projecting posteriorly of posterior margin of valve; interior of brachial valve with narrow, thickened, anacline pseudointerarea, strongly grooved by growth-lines, elevated above the valve floor anteriorly and smoothly arched postermedially to form rounded, convex fold of shell; interior of brachial valve with faint median septum and two lateral ridges; median septum low, rounded, narrow posteriorly but becoming slightly wider anteriorly and running about 50% of valve length; elongately oval muscle scars, 0·9 mm long × 0·3 mm wide, impressed posterolaterally on valve floor and diverging anteriorly at 45° with median axis of valve.

Holotype. Pedicle valve, BB 95414: length 3·4 mm, width 4·0 mm. Fig. 57.

		length	width (mm)
Paratypes.	Incomplete pedicle valve; BB 95416	3·3	–
	Brachial valve; BB 95415	3·7	3·8
	Brachial valve; BB 95606	2·8	2·8
	Incomplete brachial valve; BB 95417	–	3·6

Type horizon and locality. Loc. 1.

Genus *MULTISPINULA* Rowell, 1962

Multispinula attenuata sp. nov.

Figs 62–65

Diagnosis. Medium-sized, elongately oval *Multispinula*, about three-quarters as wide as long with narrowly rounded posterior margin; ventral pseudointerarea narrow, procline; interior of brachial valve with short median septum.

Name. 'Thinned, narrowed'.

Description. Elongately oval, dorsibiconvex *Multispinula*, estimated to have attained a maximum length of about 8 mm and a maximum width of 6 mm, anterior margin smoothly rounded, lateral margins rounded, subparallel, tapering slightly posteriorly to narrow, narrowly-rounded, posterior margin; external surfaces marked by concentric growth-lines becoming lamellose peripherally and bearing rows of pustules and hollow, prone spines; pedicle foramen apical, elongately tear-shaped, about 45% as wide as long, and estimated to have been about 40% as long as maximum shell length, with smoothly rounded anterior margin and gently rounded lateral margins tapering posteriorly; posterior margin of pedicle foramen closed by plate which projects obliquely anterodorsally through thickened umbo to form posterior margin of subcircular pedicle tube on inner surface of valve; ventral beak small, triangular, projecting posteriorly to overhang narrowly triangular, procline pseudointerarea divided into narrow triangular propareas by faint median intertrough.

Brachial valve with narrow, thickened pseudointerarea, elevated slightly medially to form low, rounded, convex ridge; floor of brachial valve with low, narrow median septum.

Holotype. Incomplete pedicle valve, BB 95409. Fig. 62.

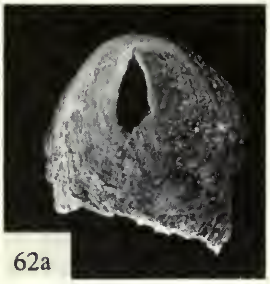
Paratypes. Incomplete pedicle valves, BB 95411, 95605; incomplete brachial valves, BB 95410, 95412.

Type horizon and locality. Loc. 1.

Discussion. While *M. attenuata* is represented by only a small number of specimens in the Tourmakeady residues, it is sufficiently distinctive to warrant specific identification. *M. attenuata* can readily be distinguished from the other, more common, Tourmakeady species, *M. hibernica*, by its elongate oval shape, proportionately narrower pedicle foramen, and narrower, procline ventral pseudointerarea divided medially by a faint intertrough. Furthermore, there is no sign, in brachial valves of *M. attenuata*, of the pair of lateral ridges which flank the dorsal median septum in *M. hibernica*.

The combination of strongly rounded posterior margin, elongately oval shape, partly closed pedicle foramen, and procline ventral pseudointerarea serves to distinguish *M. attenuata* from previously-described species of *Multispinula*. Thus, *M. subradiata* (Cooper), from the Middle Ordovician Arline formation of Tennessee (Cooper 1956: 269), differs from the new species in having a ventral valve with a strongly acuminate posterior margin and a proportionately longer and narrower pedicle foramen. The brachial valves of the two species are also readily distinguishable, as *M. subradiata* has a strong dorsal sulcation.

M. cryptotreta Goryanskiĭ, from the Cambro-Ordovician deposits of the Russian Platform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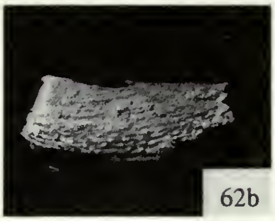
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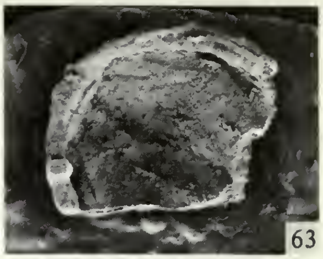
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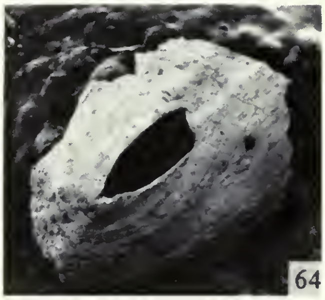
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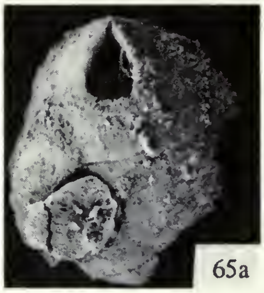
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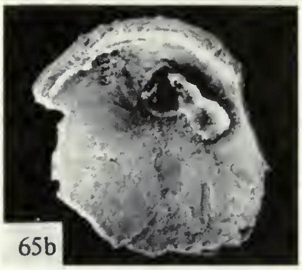
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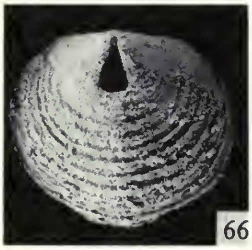
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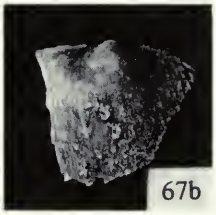
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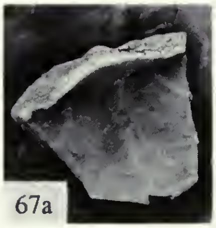
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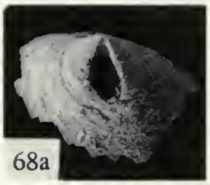
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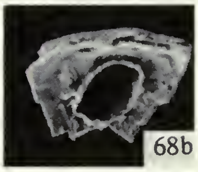
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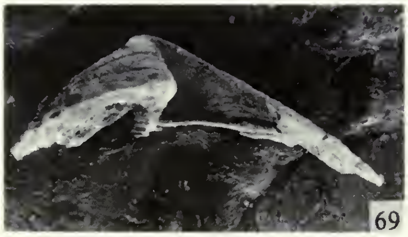
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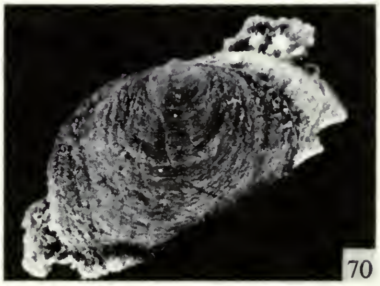
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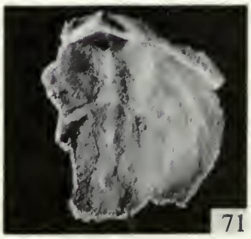
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Figs 62–65 *Multispinula attenuata* sp. nov. Fig. 62a, b, **holotype** BB 95409, exterior of incomplete pedicle valve: a, ventral view, ×7; b, lateral view ×7; Fig. 63, paratype BB 95410, interior of incomplete brachial valve, ×9; Fig. 64, paratype BB 95411, oblique view of exterior of incomplete pedicle valve, ×9; Fig. 65a, b, paratype BB 95605, exterior and interior of incomplete pedicle valve, both ×6.

Figs 66–71 *Multispinula hibernica* (Reed). Fig. 66, BB 95400, exterior of pedicle valve, ×8; Fig. 67a, b, BB 95401, interior and exterior of incomplete brachial valve: a, ×9; b, ×7. Fig. 68a, b, BB 95404, exterior and interior of incomplete pedicle valve, both ×7; Fig. 69, BB 95402, lateral view of incomplete pedicle valve showing pedicle tube, ×19; Fig. 70, BB 95403, exterior of incomplete brachial valve, ×8; Fig. 71, BB 95604, interior of incomplete brachial valve, ×6.

(Goryanskiĭ 1969: 96), differs from *M. attenuata* in having a subtriangular brachial valve with a tapering, acuminate, posterior margin. The pedicle valve of *M. cryptotreta* has not been figured, but would, on the evidence of figured brachial valves, certainly differ from that of the Irish species at least in the shape of the posterior margin.

Multispinula hibernica (Reed)

Figs 66–71

1909 *Acrotreta* ? *hibernica* Reed *in* Gardiner & Reynolds: 150; pl. 6, figs 13a–c.

Diagnosis. Subcircular, ventribiconvex *Multispinula*, with tear-shaped pedicle foramen about one-quarter as long as valve; broadly triangular ventral pseudointerarea divided medially by faint ridge; brachial interior with low, narrow, median septum and two pairs of short, divergent lateral ridges.

Description. Medium-sized, subcircular, ventribiconvex *Multispinula*, about 90% as long as wide, with obtusely rounded posterior margin and smoothly rounded anterior and lateral margins; external surfaces with concentric growth-lines becoming strongly lamellose peripherally and bearing pustules and regular rows of prone, hollow spines up to 35 μm in diameter.

Pedicle valve low to moderately conical, about one-third as high as long, with apex situated posteriorly; pedicle foramen apical, tear-shaped, about 60% as wide as long and about 25% as long as valve, smoothly rounded anteriorly and laterally but tapering sharply posteriorly to minute triangular beak; posterior margin of pedicle foramen closed by plate projecting obliquely anterodorsally through thickened ventral umbo to form posterior margin of circular pedicle tube in the valve interior; inner surface of pedicle tube marked by growth-lines; ventral pseudointerarea narrow, broadly triangular, procline to catacline, and divided medially by low ridge becoming fainter dorsally; dorsal margin of pseudointerarea thickened with faint median fold.

Interior of pedicle valve with pair of circular muscle scars, 0·9 mm in diameter, impressed posterolaterally on either side of pedicle tube; pair of oval cardinal muscle scars, 1 mm long × 0·3 mm wide, impressed anterolaterally of circular muscle scars, and diverging anteriorly at 45° from median axis of valve; anteromedian wall of cardinal muscle scars thickened, occasionally elevated to form convex boss of shell on valve floor.

Brachial valve gently convex, with swollen, rounded umbo projecting posteriorly of posterior margin of valve; dorsal pseudointerarea narrow, adnate, anacline, marked by concentric growth-lines and becoming pustulose and spinose posterolaterally; pseudointerarea smoothly elevated medially, with rounded anterior margin overhanging valve floor; floor of valve with short, low, median septum extending 3 mm anteriorly from beneath pseudointerarea, with a pair of low ridges branching off at about two-thirds of its length and diverging anteriorly at 60° from median axis of valve; two short, narrow, lateral ridges additionally impressed posterolaterally on floor of valve and diverge anteriorly at 30° from median axis of valve; pair of faint, elongately oval, muscle scars, 1·2 mm long × 0·6 mm wide, impressed symmetrically within the angles subtended by the posterior pair of lateral ridges and the median septum, and diverging anteriorly at 30° from median axis of valve; two pairs of faint, oval, muscle scars, corresponding to transmedian (?) and central (?) muscles, impressed symmetrically immediately lateral of branching ridges.

Figured material. Pedicle valve: BB 95400 (length 3·3 mm, width 3·7 mm); incomplete pedicle valves: BB 95402, 95404; incomplete brachial valves: BB 95401, 95403, 95604. Loc 1.

Discussion. The genus *Multispinula* was erected to incorporate species previously assigned to *Schizambon*, but distinguished from that genus by having peripheral spines arranged regularly along the anterior margin of concentric lamellar growth-lines, a narrow ventral pseudointerarea, and an internal pedicle tube (Rowell 1962: 148). In addition, species of

Multispinula are generally about two or three times larger than most *Schizambon*. On the basis of these criteria the Tourmakeady material clearly belongs to *Multispinula*.

M. hibernica was first described, as *Acrotreta* (?) *hibernica*, by Reed (1909), who recovered a single pedicle valve and its external mould from the Tourmakeady Limestone exposed in the 'upper part of Stream F' (Reed *in* Gardiner & Reynolds 1909: 150). During the course of the present study a much larger sample was recovered from this same locality, including previously undescribed brachial valves, and an extensive revision of Reed's original description became necessary. In particular it is now clear, from an examination of his specimen (SM A10372a, b), that Reed was in error when he stated 'the apex of the valve being broken off, it is uncertain whether a foramen was present'. In fact the valve is complete, with the large apical foramen characteristic of *Multispinula*. In addition, a close examination of the ventral pseudointerarea of Reed's specimen reveals that it is divided medially by a distinct ridge rather than a 'broad median shallow groove'.

When compared with the type species of *Multispinula, M. macrothyris* (Cooper) from the Middle Ordovician Benbolt formation of Virginia (Cooper 1956: 267), *M. hibernica* differs in shape, being rounded rather than elongately oval, and has a proportionately smaller pedicle foramen and a much more conical pedicle valve. *M. hibernica* also differs in lacking a dorsal sulcus and radial ornamentation.

The posterior margin of a pedicle valve fragment of *Multispinula* sp. from the L. Ordovician Antelope Valley Limestone of southern Nevada (Krause & Rowell 1975: 68) is similar to that of *M. hibernica*, but differs in having an apsacline ventral pseudointerarea and a proportionately wider pedicle foramen.

Multispinula is also known from the Ordovician of Kazakhstan, but *M. parvula* Popov (1980: 117) is readily distinguishable from *M. hibernica*, as the former has a strong sulcation in the brachial valve and radial ornamentation.

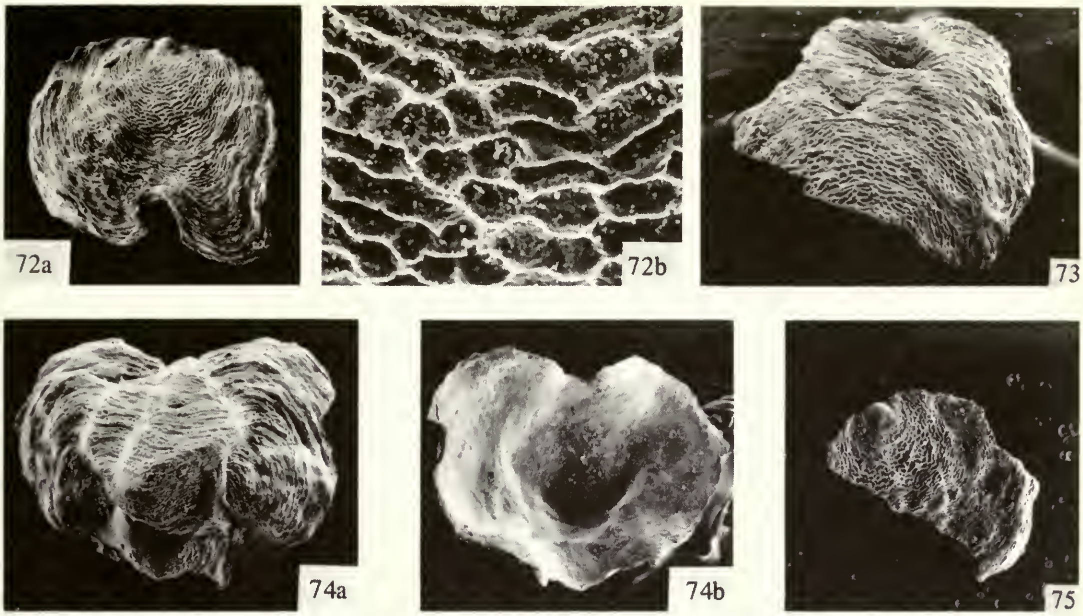
Superfamily indet.

Inarticulata, gen. et sp. indet.

Figs 72–75

The Tourmakeady Limestone exposed at Loc. 1 contained a small sample of a distinctively ornamented inarticulate species. The specimens (BB 95441–95444) are mostly incomplete, but reconstructions indicate that complete valves were very variable in shape, with a maximum dimension of about 3·5 mm. The least distorted specimen (BB 95441), which is complete and measures 1·8 mm in length × 2·2 mm in width, has an almost straight posterior margin and subparallel, irregular lateral margins. The anterior margin of this specimen is strongly bilobed, with a narrow, posteriorly rounded, anteromedian notch separating rounded, asymmetrical, anterolateral lobes. Other fragments also show evidence of an anteromedian notch. The lateral profile of these specimens is also very variable, ranging from almost flat to moderately conical. Maximum convexity is usually developed anteriorly, while the posterior and posterolateral regions of the valve are often flattened. The external surfaces are very irregular, and ornamented by fine, elevated, discontinuous, concentric fila, numbering about 40 per mm medially. The concentric fila are crossed by short, impersistent radial fila which give rise to an irregular reticulate pattern. Internally the valves are featureless, save for the hollows and ridges corresponding to the external surface irregularities.

The taxonomic affinities of these specimens are problematical. None shows evidence of attachment scars, although their distorted morphology strongly suggests a cemented mode of life. Presumably, therefore, the sample consists of the brachial valves of a genus which was cemented by a pedicle valve which has not been recovered. Cementation is common amongst the Craniacea, but all genera assigned to that superfamily are characterized by holoperipheral, or more rarely mixoperipheral, growth, while the Tourmakeady specimens clearly grew by hemiperipheral accretion. In addition, now that the Eoconulidae have been removed



Figs 72–75 Inarticulata, gen. et sp. indet. Fig. 72a, b, BB 95441, brachial(?) valve exterior: a, ×15; b, ornamentation, ×110; Fig. 73, BB 95444, brachial(?) valve fragment, ×19; Fig. 74a, b, BB 95442, exterior and interior of brachial(?) valve, both ×17; Fig. 75, BB 95443, exterior of incomplete brachial(?) valve, ×19.

from the superfamily (Krause & Rowell 1975: 798), all craniaceans are calcareous-shelled, in contrast to the chitinophosphatic shell substance of the Tourmakeady valves.

The external ornamentation of the Tourmakeady specimens is similar to that of some species of the paterinacean genus *Micromitra*. However, the brachial valve of genera assigned to the Paterinacea has a well-developed homochilidium, a feature which is not evident in the Tourmakeady specimens, effectively precluding them from that superfamily. Indeed, because of the paucity of the sample, and the absence of information on the morphology of the pedicle valve, it is impossible to assign these specimens to any established inarticulate superfamily.

Class **ARTICULATA** Huxley, 1869

Order **ORTHIDA** Schuchert & Cooper, 1932

Suborder **ORTHIDINA** Schuchert & Cooper, 1932

Superfamily **ORTHACEA** Woodward, 1852

Family **EOORTHIDAE** Walcott, 1908

Genus ***APHEOORTHIS*** Ulrich & Cooper, 1936

Apheoorthis sp.

Figs 76–79

Diagnosis. Large, semicircular to subquadrate *Apheoorthis*, about nine-tenths as long as wide, external surfaces multicostellate with 5 ribs per mm at 5 mm anteromedially of dorsal umbo.

Description. Large, semicircular to subquadrate *Apheoorthis*, estimated to have attained a maximum length of about 10 mm and to be about 90% as long as wide; external ornamentation multicostellate with 5 rounded ribs per mm at 5 mm anteromedially of dorsal umbo; ventral interarea very narrow, apsacline, with open delthyrium; dorsal interarea very narrow, anacline.

Ventral interior with well-defined converging dental plates sloping down to valve floor to define narrow, posteriorly-tapering, elongately subtriangular, tripartite pseudospondylium with narrow, tongue-shaped, median adductor scar and measuring 2·2 mm × 1·6 mm in one specimen.

Figured material. Incomplete conjoined valves, BB 95586; incomplete pedicle valves, BB 95583–5. Loc. 1.

Discussion. *Apheoorthis* is sparsely represented in the Tourmakeady residues, and not much reliable information can be ascertained about the dorsal interior. However, the presence of a well-defined, tripartite pseudospondylium in the pedicle valve, combined with characteristic shell outline and profile, suggests that these specimens can be assigned to *Apheoorthis*. A comparison with previously-described species of *Apheoorthis* from North America, such as *A. ornata* Ulrich & Cooper (1938: 86) from the Lower Ordovician of Oklahoma, confirms the similarity in the internal morphology of the pedicle valve. The Irish specimens appear to be much more finely multicostellate than those from North American successions, many of which are also fascicostellate. Specific recognition of the Tourmakeady specimens, however, has been withheld until the internal morphology of the brachial valve is known.

Family **HESPERONOMIIDAE** Ulrich & Cooper, 1936

Genus ***PROTOHESPERONOMIA*** nov.

Diagnosis. Small, transversely subquadrate to semicircular hesperonomiid, pedicle valve gently convex becoming geniculate when adult; brachial valve gently concave to planar when juvenile, becoming gently to moderately convex in later growth stages; external ornamentation unequally parvicostellate composed of fine, rounded, ribs divided into narrowly triangular sectors by a thickening of regularly-spaced primary ribs.

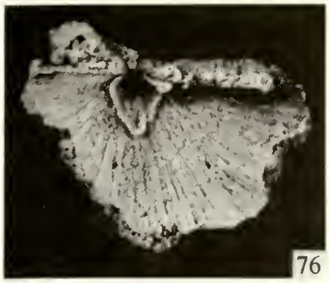
Ventral interior with small triangular teeth supported by curved dental plates, widely divergent dorsally but becoming subparallel ventrally and forming posterolateral margins of strongly bilobed ventral muscle platform; ventral mantle canal system unknown.

Dorsal interior with long, thin, flat-lying brachiophores, diverging anteriorly and flanked laterally by shallow, narrowly-triangular sockets; brachiophores supported by weak, convergent brachiophore bases united with floor of valve to form poorly-defined, flat-lying, narrowly triangular notothyrial platform; dorsal mantle canal system unknown.

Name. An early relative of *Hesperonomia*.

Type species. *Protohesperonomia resupinata* sp. nov. from the Tourmakeady Limestone, Co. Mayo.

Discussion. The Tourmakeady residues yielded a number of shells with a well-defined unequally parvicostellate ornamentation, characterized internally by simple brachiophores and strongly bilobed ventral muscle scars. These features, along with the narrow profile of the shells, indicate that the affinities of these specimens lie with the Hesperonomiidae. Within this small family, the new Irish genus is most similar to *Hesperonomia* Ulrich & Cooper in the form of the dorsal cardinalia. However, *Hesperonomia* is readily distinguished from *Protohesperonomia* by the presence of a prominent cardinal process which is not seen in any of the Irish specimens. Furthermore, the lateral muscle scars in the ventral valve of *Hesperonomia* are not so well developed, and the ventral muscle field in this genus has a subquadrate outline rather than the 'tuning-fork' shape of *Protohesperonomia*. Externally the new genus is also readily distinguishable, as a well-defined, unequally parvicostellate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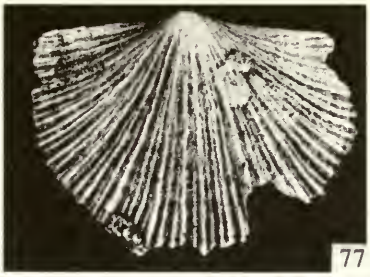
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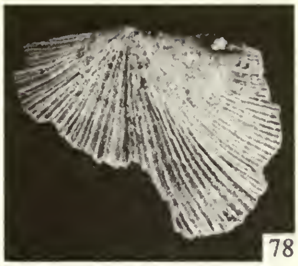
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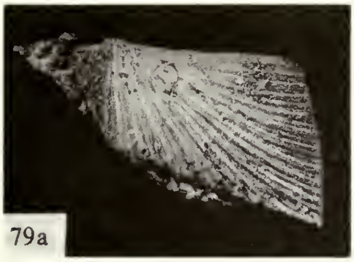
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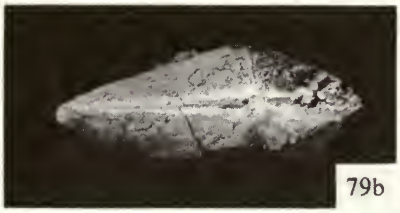
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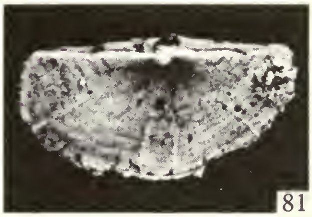
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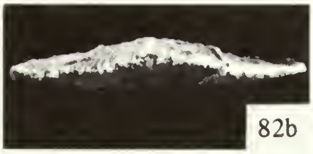
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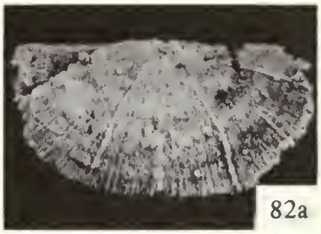
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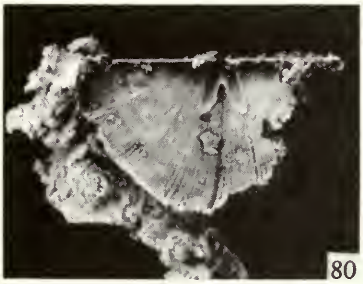
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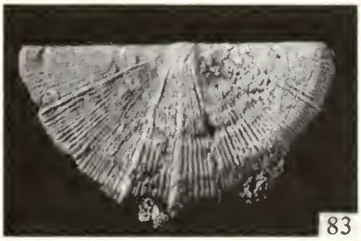
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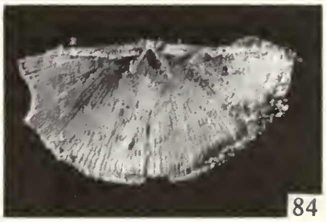
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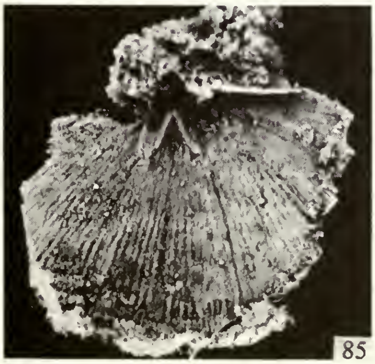
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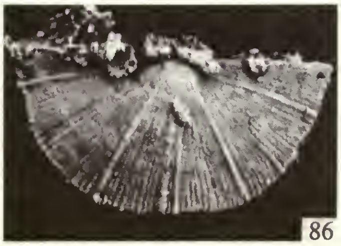
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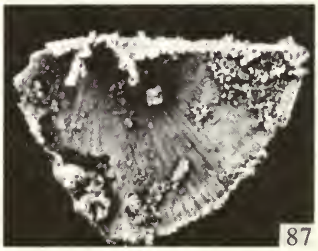
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Figs 76–79 *Apheoorthis* sp. Fig. 76, BB 95585, interior of incomplete pedicle valve, ×4; Fig. 77, BB 95583, exterior of incomplete pedicle valve, ×8; Fig. 78, BB 95584, exterior of incomplete pedicle valve, ×3; Fig. 79a, b, BB 95586, ventral and posterior views of incomplete conjoined valves, both ×4.

Figs 80–87 *Protohesperonomia resupinata* gen. et sp. nov. Fig. 80, **holotype** BB 95502, interior of incomplete pedicle valve, ×6; Fig. 81, paratype BB 95504, dorsal view of juvenile conjoined valves, ×7; Fig. 82a, b, paratype BB 95507, ventral and anterior views of juvenile conjoined valves, both ×8; Fig. 83, paratype BB 95505, exterior of resupinate pedicle valve, ×5; Fig. 84, paratype BB 95503, interior of brachial valve, ×5; Fig. 85, paratype BB 95508, interior of incomplete pedicle valve, ×6; Fig. 86, paratype BB 95509, ventral view of conjoined valves, ×6; Fig. 87, paratype BB 95506, interior of incomplete brachial valve, ×6.

ornamentation and peripheral geniculation are features not seen in other hesperonomiid genera.

Protohesperonomia is at present monospecific, and known only from the Tourmakeady Limestone.

Protohesperonomia resupinata sp. nov.

Figs 80–87

DIAGNOSIS. Small, transversely subquadrate to semicircular *Protohesperonomia* averaging 50% as long as wide, gently convex pedicle valve becoming geniculate when adult and with a maximum thickness averaging 38% of valve length, brachial valve gently concave to planar when juvenile, becoming gently to moderately convex when adult, averaging 25% as deep as long; external ornamentation unequally parvicostellate with 8–9 rounded ribs per mm at 2 mm anteromedially of dorsal umbo and divided into narrowly triangular sectors by a thickening of every seventh to tenth rib.

NAME. 'Lying on its back'.

DESCRIPTION. Small, transversely subquadrate to semicircular *Protohesperonomia* averaging 50% as long as wide ($\bar{l}$ mm (var l) 3·53 (0·71), $\bar{w}$ mm (var w) 7·03 (3·51), r = 0·992; n = 11), pedicle valve gently convex averaging in 2 valves 20% as deep as long when juvenile but becoming geniculate when adult and averaging 38% as deep as long (range 36–41%; n = 3); brachial valve gently concave to planar when juvenile becoming gently to moderately convex when adult, attaining a maximum thickness averaging 25% of valve length (range 24–26%; n = 3); cardinal extremities acutely rounded, lateral and anterior margins smoothly rounded, brachial valve with broad, gently rounded, median sulcus corresponding to subdued median carina on pedicle valve and bearing one or two swollen ribs medially; external ornamentation unequally parvicostellate with 8 and 9 rounded ribs per mm at 2 mm anteromedially of umbones of 1 and 2 brachial valves respectively, and divided into narrowly triangular sectors by a thickening of every seventh to tenth rib; ventral interarea narrow, planar, catacline, with open delthyrium, dorsal interarea narrow, planar, anacline, notothyrium open.

Ventral interior with small triangular teeth supported by curved dental plates widely divergent dorsally but becoming subparallel ventrally and forming posterolateral margins of strongly bilobed ventral muscle field extending anteriorly for an average of 29% (range 28–31%; n = 4) of valve length, defined by elevated rims of shell and composed of two anteriorly rounded lobes diverging anteriorly at 30° with median axis of valve and each averaging 27% as long as wide; lobes of ventral muscle field uniting posteromedially on either side of small, elevated, rounded, posteriorly tapering boss of shell.

Dorsal interior with thin, flat-lying brachiophores diverging anteriorly at angle of 60°, extending anteriorly for an average of 25% of valve length in 2 valves and flanked laterally by shallow, narrowly triangular sockets, brachiophores supported by weak, convergent brachiophore bases united with floor of valve to form poorly-defined, flat-lying, narrowly triangular notothyrial platform, rounded anteriorly and with dimensions of 0·7 × 0·6 mm and 0·7 × 0·7 mm in 2 specimens.

HOLOTYPE. Incomplete pedicle valve; BB 95502. Fig. 80.

		length	width (mm)
PARATYPES.	Conjoined valves; BB 95504a, b	3·0	5·3
	Conjoined valves; BB 95507a, b	2·7	6·1
	Conjoined valves; BB 95509a, b	3·6	6·7
	Pedicle valve; BB 95505	4·8	9·1
	Incomplete pedicle valve; BB 95508	5·8	–
	Brachial valve; BB 95503	4·1	–
	Incomplete brachial valve; BB 95506	4·5	–

TYPE HORIZON AND LOCALITY. Loc. 1.

Family **ORTHIDIELLIDAE** Ulrich & Cooper, 1936

Genus ***ORTHIDIUM*** Hall & Clarke, 1892

Orthidium cf. ***gemmiculum*** (Billings)

Figs 88–90

cf. 1865 *Orthis gemmicula* Billings: 75
cf. 1892 *Orthidium gemmicula* (Billings) Hall & Clarke: 217
cf. 1938 *Orthidium gemmiculum* (Billings); Ulrich & Cooper: 112

Diagnosis. Small, subcircular to transversely oval *Orthidium*, with a moderately to strongly convex pedicle valve averaging 90% as long as wide and 34% as deep as long, and a smoothly convex brachial valve averaging 77% as long as wide and 47% as deep as long; ornamented by 8–9 rounded ribs per mm at 2 mm anteromedially of dorsal umbo, and regularly-spaced concentric lamellae extended peripherally as frills.

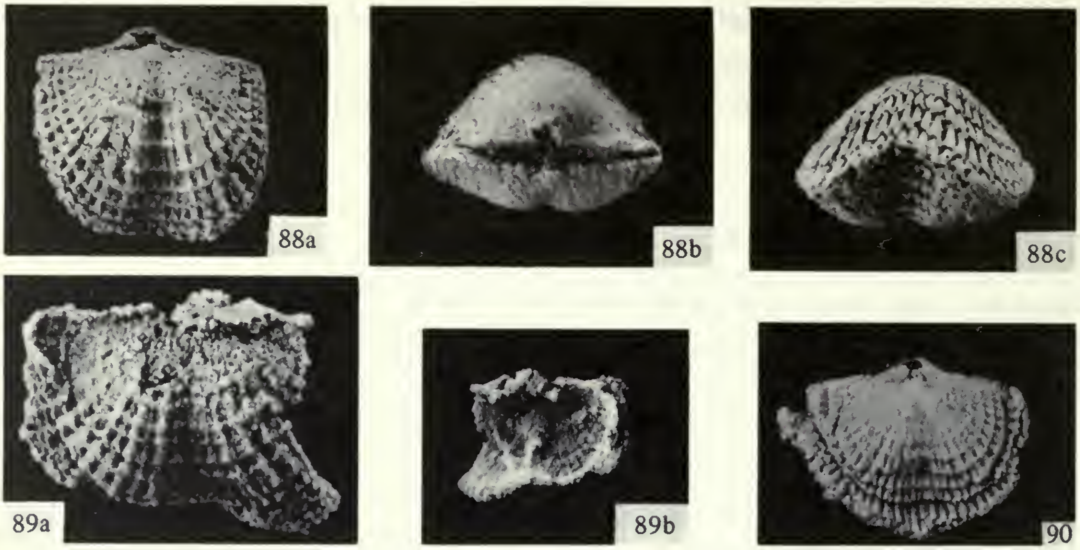
Description. Small subcircular to transversely oval *Orthidium*; pedicle valve moderately to strongly convex, averaging 90% as long as wide (range 86–95%; n = 4) and 34% as deep as long (range 31–36%; n = 4); brachial valve smoothly convex, averaging 77% as long as wide (range 75–82%; n = 4) and with a maximum depth averaging 47% of valve length (range 42–53%; n = 4) developed at strongly sulcate anteromedian margin; lateral margins of both valves smoothly rounded, anterior margins bilobed by sulcation; external ornamentation costellate with 8 and 9 rounded ribs per mm at 2 mm anteromedially of umbones of 2 and 4 brachial valves respectively, costellae crossed by regularly-spaced concentric lamellae with an average separation of 0·3 mm (range 0·3–0·4 mm) and 0·26 mm (range 0·2–0·3 mm) along the median axis of two adult brachial valves, concentric lamellae strongly developed in later growth stages and extending peripherally up to one mm as thin, flat-lying, concentric frills; brachial valve with well-developed rounded sulcus with an average maximum width of 1·1 mm in 4 adult brachial valves (range 0·9–1·2 mm); ventral interarea triangular, curved, apsacline with open delthyrium, dorsal interarea very narrow, anacline.

Ventral interior with large, thickened, triangular teeth flanked by well-developed crural fossettes and supported by erect dental plates obscured by callus deposits.

Dorsal interior with massive, tongue-shaped, cardinal process with dimensions of 0·6 × 0·7 mm and 0·7 × 0·8 mm in two specimens and recurved posteriorly to occupy delthyrium of pedicle valve in conjoined valves; brachiophores narrowly triangular, thickened, erect, extending ventrally 0·6 mm above valve floor in one specimen, and united laterally with cardinal process by callus deposits to form massive unified cardinalia flanked by broadly triangular sockets; floor of valve with low rounded ridge extending anteriorly for 1·5 mm and 1·9 mm in two adult valves; two pairs of adductor scars impressed on floor of valve extending forwards for about 48% of the length of the valve and symmetrically disposed on either side of median ridge and defined laterally by low elevated ridges, posterior pair tear-shaped, and with median axis inclined at 45° to median axis of valve, anterior pair elongately oval and subparallel with median axis of valve.

Figured material. Conjoined valves, BB 95466a, b (length 2·6 mm, width 2·9 mm), BB 95468 (length 3·1 mm, width 3·6 mm); brachial valve BB 95467. Loc. 1.

Discussion. Although sparsely represented in the Tourmakeady residues, the diagnostic features of *Orthidium* are so striking that its recognition is unequivocal. In particular the massive cardinalia and distinctive concentric lamellose ornamentation are diagnostic of this relatively rare genus. *Orthidium* is known primarily from North America, having been recorded from low–middle Ordovician successions in Quebec, Newfoundland, and Nevada. Previously-described species display many morphological similarities, but there are details of shell proportion and ornamentation which distinguish them and which confirm the close affinity between the Irish specimens and *O. gemmiculum* from the Lower Ordovician Levis Shales of Quebec (Ulrich & Cooper 1938: 112). Thus the length/width ratios for the pedicle



Figs 88–90 *Orthidium* cf. *gemmiculum* (Billings). Fig. 88a, b, c, BB 95466, dorsal, posterior and anterior views of conjoined valves, all ×11; Fig. 89a, b, BB 95467, exterior and anterior views of incomplete brachial valve; a, ×16; b, ×10. Fig. 90, BB 95468, dorsal view of conjoined valves, ×8.

and brachial valve of the Canadian species are 86% and 75% respectively, as compared with 90% and 77% respectively for the Irish specimens. Canadian *O. gemmiculum* is slightly more finely costellate than the present Irish representatives but, in the absence of other distinguishing features, this difference is not considered sufficient to form the basis of a new taxon. The other described species are considerably more coarsely costellate than the Quebec and Irish specimens.

Family **ORTHIDAE** Woodward, 1852

Subfamily **ORTHINAE** Woodward, 1852

Genus ***ARCHAEORTHIS*** Schuchert & Cooper, 1931

Archaeorthis globosa sp. nov.

Figs 91–94

Diagnosis. Small, transversely oval to subquadrate *Archaeorthis* with slight inward geniculation in adult shells, pedicle valve moderately to strongly convex averaging 59% as long as wide and 39% as deep as long, brachial valve strongly convex posteromedially, becoming gently convex peripherally, and averaging 56% as long as wide and 37% as deep as long; external ornamentation fascicostellate with 5–7 ribs per mm at 2 mm anteromedially of dorsal umbo.

Name. 'Rounded'.

Description. Small, transversely oval to subquadrate, ventribiconvex *Archaeorthis*; pedicle valve moderately to strongly convex averaging 59% as long as wide and 39% as deep as long ($\bar{l}$ mm (var l) 2·35 (0·833), $\bar{w}$ mm (var w) 3·91 (1·77), r = 0·965; n = 77. $\bar{l}$ mm (var l) 3·32 (0·199), $\overline{th}$ mm (var th) 1·28 (0·043), r = 0·860; n = 16); brachial valve strongly convex postermedially becoming gently convex peripherally and averaging 56% as long as wide and with a maximum thickness developed at sulcate anterior margin averaging 37% of valve length ($\bar{l}$ mm (var l) 2·17 (0·961), $\bar{w}$ mm (var w) 3·98 (1·828), r = 0·937; n = 68. $\bar{l}$ mm (var l) 3·01 (0·890), $\overline{th}$ mm (var th) 1·12 (0·472), r = 0·847; n = 12); peripheral margins of adult valves smoothly rounded with slight inward geniculation; external ornamentation fascicostellate with 5, 6 and 7 ribs per mm at 2 mm anteromedially of umbones 14, 15 and 9 brachial valves, respectively; brachial valve with narrow angular sulcus very faint posteriorly but becoming broader anteriorly to average 1·1 mm in width (range 0·9–1·2 mm; n = 18) at 2 mm anteromedially of dorsal umbo, and corresponding to moderately or strongly defined carina on pedicle valve; ventral interarea triangular, gently curved, apsacline to catacline, with open delthyrium; dorsal interarea narrow, anacline.

Ventral interior with short triangular teeth extending dorsally for an average of 18% (range 15–20%; n = 5) of the length of the ventral interarea and supported by short, strongly receding, subparallel dental plates; ventral muscle field equidimensional to transversely oval, averaging 92% as long as wide (range 78–100%; n = 5) and defined anteriorly by elevated, anteriorly convex, rim buttressed by prominent, elongate, anteriorly sloping, posteriorly tapering, callus averaging 62% as wide as long ($\bar{l}$ mm (var l) 1·44 (0·049), $\bar{w}$ mm (var w) 0·90 (0·047), r = 0·887; n = 13); up to 3 narrow branches, 0·1–0·2 mm in diameter, of digitate mantle canal system impressed posterolaterally of median callus.

Dorsal interior with flattened, blade-like, blunt, divergent brachiophores extending for 53% and 29% of valve length in two specimens, flanked by narrow, triangular sockets; notothyrial platform triangular, equidimensional to transversely elongate, on average 90% as long as wide ($\bar{l}$ mm (var l) 0·607 (0·005), $\bar{w}$ mm (var w) 0·68 (0·006), r = 0·685; n = 14) buttressed by low, rounded, median ridge extending anteriorly on average for 65% of valve length (range 56–74%; n = 5); floor of valve with two pairs of adductor scars impressed symmetrically on either side of median ridge; anterior pair elongately oval with long axis aligned parallel with median ridge and averaging 55% as wide as long (range 50–58%; n = 4); posterior pair of adductor scars tear-shaped, tapering posteriorly, on average 65% as wide as long (range 62–67%; n = 3) with longitudinal axes diverging anteriorly at angle of 50° from median axis of valve.

HOLOTYPE. Pedicle valve, BB 95461: length 2·9 mm, width 5·0 mm. Fig. 91.

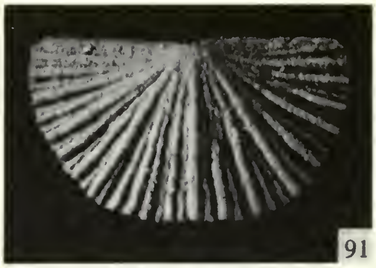
		length	width (mm)
PARATYPES.	Conjoined valves; BB 95463a, b	3·6	5·4
	Pedicle valve; BB 95464	3·4	5·0
	Brachial valve; BB 95462	2·8	4·0
	Incomplete brachial valve; BB 95465	–	–

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. It is noteworthy that the sample of *Archaeorthis* recovered from the Tourmakeady Limestone includes a preponderance of complete conjoined valves, which have afforded an unusually comprehensive understanding of the morphology of the species.

Archaeorthis is known mainly from the older Ordovician successions in North America, but the Irish specimens can confidently be assigned to this genus by virtue of the diagnostic association of premuscular callosity in the pedicle valve and orthid cardinalia. The peripheral geniculation, along with details of ornamentation and shell shape, immediately distinguishes *A. globosa* from previously-described species of the genus. Apart from lacking geniculation, North American species generally have a costellate ornamentation and a prominent ventral umbo. In addition the strongly transversely oval outline of *A. globosa* differs markedly from the elongately oval or slightly transversely oval shape of North American stocks.

A. subcarinata (Laurie 1980: 16), from the Lower Ordovician of Australia, is readily distinguished by its subcircular outline, absence of geniculation, and much finer ribbing. *A. pribyli* (Havlíček 1949), from the late Arenig of Bohemia, is also distinguished from *A. globosa* by its subcircular outline and lack of peripheral geniculation.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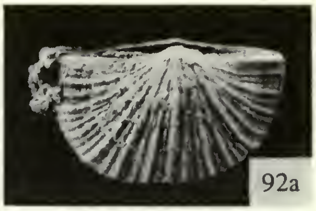
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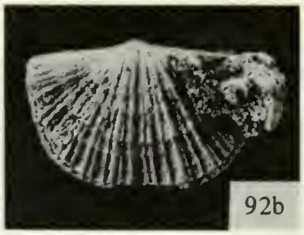
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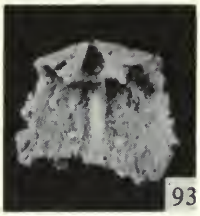
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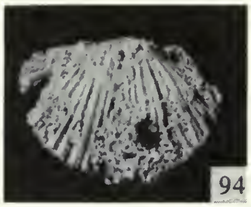
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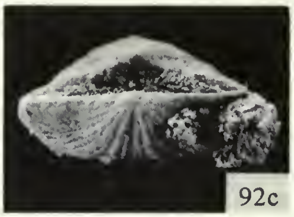
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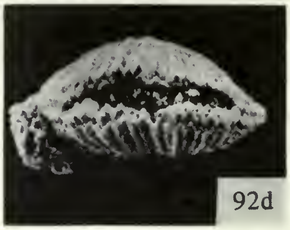
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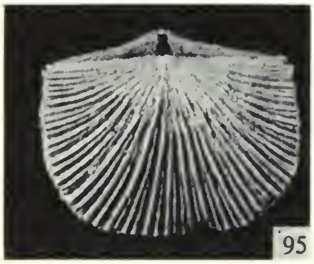
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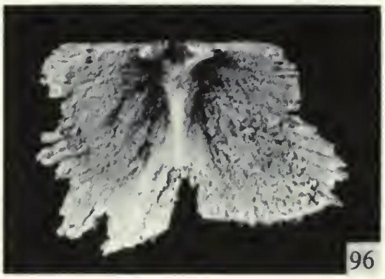
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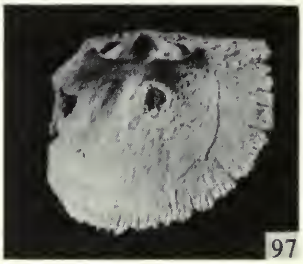
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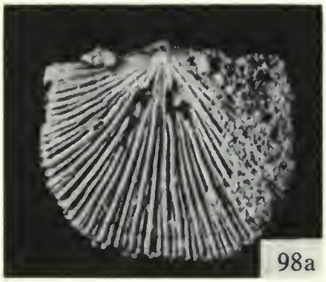
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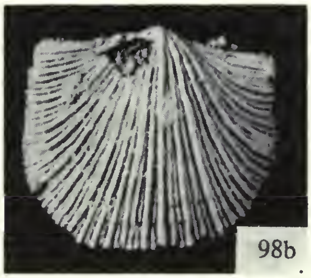
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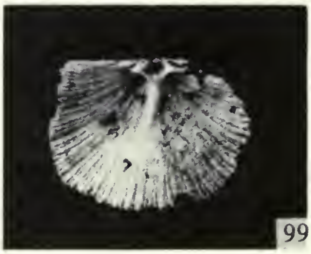
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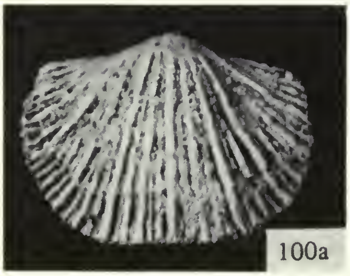
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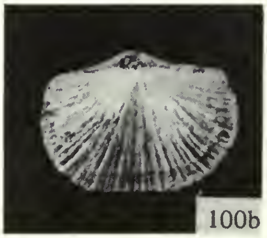
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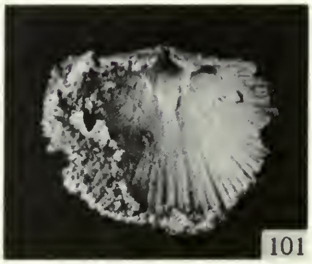
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Figs 91–94 *Archaeorthis globosa* sp. nov. Fig. 91, **holotype** BB 95461, exterior of pedicle valve, ×8; Fig. 92a, b, c, d, paratype BB 95463, ventral, dorsal, oblique posterior and anterior views of conjoined valves, all ×6; Fig. 93, paratype BB 95565, interior of incomplete brachial valve, ×7; Fig. 94, paratype BB 95462, exterior of incomplete brachial valve, ×7.

Figs 95–101 *Nothorthis pennsylvanica* Ulrich & Cooper. Fig. 95, BB 95593, dorsal view of conjoined valves, ×5; Fig. 96, BB 95599, interior of incomplete brachial valve, ×7; Fig. 97, BB 95595, interior of incomplete brachial valve, ×4; Fig. 98a, b, BB 95598, dorsal and ventral views of conjoined valves, ×6; Fig. 99, BB 95596, interior of incomplete brachial valve, ×4; Fig. 100a, b, BB 95597, ventral and dorsal views of conjoined valves: a, ×8; b, ×5; Fig. 101, BB 95594, interior of pedicle valve, ×4.

Genus *NOTHORTHIS* Ulrich & Cooper, 1938

Nothorthis pennsylvanica Ulrich & Cooper

Figs 95–101

1938 *Nothorthis pennsylvanica* Ulrich & Cooper: 107

Diagnosis. Medium-sized, transversely oval or semicircular to subquadrate *Nothorthis*, pedicle valve moderately to strongly convex, averaging 73% as long as wide and 41% as deep as long; brachial valve gently convex, averaging 69% as long as wide and 25% as deep as long; external ornamentation multicostellate, with 5 to 8 ribs per mm at 5 mm anteromedially of dorsal umbo.

Description. Medium-sized, transversely oval or semicircular to subquadrate ventribiconvex *Nothorthis*; pedicle valve moderately to strongly convex, averaging 73% as long as wide and 41% as deep as long ($\bar{l}$ mm (var l) 3·81 (0·715), $\bar{w}$ mm (var w) 5·20 (0·818), r = 0·863; n = 70. $\bar{l}$ mm (var l) 5·25 (0·529), $\overline{th}$ mm (var th) 2·17 (0·111), r = 0·767; n = 21); brachial valve gently convex to almost plane, averaging 69% as long as wide and 25% as deep as long ($\bar{l}$ mm (var l) 3·92 (0·520), $\bar{w}$ mm (var w) 5·67 (0·682), r = 0·809; n = 50. $\bar{l}$ mm (var l) 4·84 (0·543), $\overline{th}$ mm (var th) 1·30 (0·178), r = 0·715; n = 10); lateral margins of both valves strongly and evenly rounded, anterior margins smoothly and gently rounded; external ornamentation multicostellate, with ribs branching predominantly internally (e.g. $1\bar{a}\bar{1}$, $1\bar{a}$, $1\bar{b}$, 1, $2\bar{a}\bar{1}$, $2\bar{a}$, $2\bar{b}$, 2, $3\bar{a}\bar{1}$, $3\bar{a}$, $3\bar{b}$, 3), only rarely branching externally (e.g. $3\mathring{a}$ first external in 5 out of 12 brachial valves), ribs numbering 5–8 per mm at 5 mm anteromedially of umbo of 5, 8, 3 and 1 brachial valves respectively; brachial valve with shallow, smoothly rounded sulcus, narrow posteriorly but becoming broader anteriorly; ventral interarea narrow, curved, apsacline, with open delthyrium, dorsal interarea narrow, anacline.

Ventral interior with thickened triangular teeth extending anteriorly on average for 19% of valve length ($\bar{l}$ mm (var l) 5·28 (0·551), $\bar{l}_{te}$ mm (var l_{te}) 0·97 (0·030), r = 0·542; n = 16) supported by short, curved, receding, divergent dental plates; floor of valve with undifferentiated, slightly elevated, muscle attachment platform, tongue-shaped to elongately oval in outline, with moderately thickened anterior and anterolateral margins, on average 81% as wide as long ($\bar{l}$ mm (var l) 1·16 (0·067), $\bar{w}$ mm (var w) 0·94 (0·054), r = 0·902; n = 22).

Dorsal interior with blunt, thickened brachiophores, triangular in cross section, flanked by deep, oblique triangular sockets defined anterolaterally by slightly elevated anterior margin of triangular, concave, fulcral plates; brachiophore bases extending on average for 12% of valve length ($\bar{l}$ mm (var l) 4·77 (0·609), $\bar{l}_b$ mm (var l_b) 0·62 (0·022), r = 0·855; n = 10) and 34% of lateral extension of sockets ($\bar{l}_b$ mm (var l_b) 0·62 (0·016), $\bar{w}_{so}$ mm (var w_{so}) 1·83 (0·164), r = 0·777; n = 13); notothyrial platform well-defined, thickened, transversely oval to semicircular, on average 81% as long as wide ($\bar{l}_n$ mm (var l_n) 0·59 (0·020), $\bar{w}_n$ mm (var w_n) 0·73 (0·015), r = 0·630; n = 18); floor of valve with short, low, median ridge extending on average for 39% of valve length ($\bar{l}$ mm (var l) 4·49 (0·739), $\bar{l}_s$ mm (var l_s) 1·76 (0·204), r = 0·841; n = 14); dorsal muscle scars poorly defined, consisting of two pairs of elongately oval scars measuring 0·6 × 0·3 mm in two valves, situated posterolaterally on valve floor and flanking median ridge.

		length	width (mm)
Figured material.	Conjoined valves; BB 95593a, b	5·0	5·9
	Conjoined valves; BB 95597a, b	3·6	5·3
	Conjoined valves; BB 95598a, b	5·0	5·6
	Pedicle valve; BB 95594	4·9	6·4
	Brachial valve; BB 95595	6·2	–
	Brachial valve; BB 95596	4·6	–
	Incomplete brachial valve; BB 95599	–	–

All Loc. 1.

Discussion. *Nothorthis* is a rare genus, although it is one of the most abundant constituents of the Tourmakeady fauna. Previously described species display a high degree of morphological similarity, so that distinction between different stocks is likely to depend on quantitatively defined characteristics. So far such data exist only for the Tourmakeady specimens which do, however, compare very closely with *N. pennsylvanica* Ulrich & Cooper, from the Lower Ordovician Beeksmantown Formation of south-eastern Pennsylvania, in the nature of the cardinalia and in the shell proportions of the figured specimens of the American stock. Ulrich & Cooper (1938: 107) considered the slightly elevated ventral muscle platform of *N. pennsylvanica* to be diagnostic of the species and, in this feature, the Irish and American valves are indistinguishable.

A feature of the statistical data derived for the Tourmakeady *Northorthis* is the high degree of variability in shape parameters, as reflected in the relatively low values for the coefficient of correlation (r). This variability is discernible both in the shape of the shell and in internal structures. The variability is partly an expression of the relatively narrow size range of the stock; but there is also an inherently greater morphological variability than usual in most features. However, attempts to isolate separate sub-groups within the Tourmakeady sample on the basis of shell proportions failed, in the face of demonstrable gradations from, for example, strongly transversely oval shells to semicircular or occasionally elongately oval ones.

Genus ***ORTHAMBONITES*** Pander, 1830

Orthambonites cf. ***panderiana*** (Hall & Clarke)

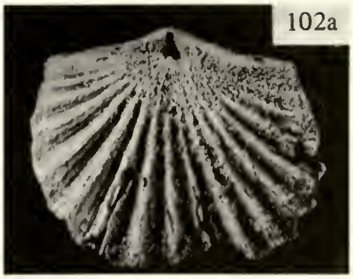
Figs 102–106

cf. 1865 '*Orthis orthambonites* (Pander)' Billings: 77; *non* von Buch 1838, *nec O. calligramma* var. *orthambonites* de Verneuil *in* Murchison 1845.
cf. 1890 *Orthis orthambonites* "Pander sp." Billings; Schuchert: 43.
cf. 1892 *Orthis orthambonites* Billings, *non* von Buch; Hall & Clarke: 221.
cf. 1892 *Orthis panderiana* Hall & Clarke: pl. 5, footnote.
cf. 1894 *Orthis panderiana* Hall & Clarke; Hall & Clarke: 338.
cf. 1938 *Orthis panderiana* Hall & Clarke; Ulrich & Cooper: 102 (*cum syn.*)

Diagnosis. Small, subquadrate to transversely ovate *Orthambonites*, with a moderately to strongly convex pedicle valve averaging 74% as long as wide and 46% as deep as long and a brachial valve averaging 70% as long as wide and 24% as deep as long; ornamented by 15–19 angular ribs with a wavelength of about one mm, 5 mm anteromedially of ventral umbo; ventral muscle field triparite, with elongate median adductor scar extending anteriorly beyond flanking diductors.

Description. Small, subquadrate to transversely ovate, ventribiconvex *Orthambonites*; moderately to strongly convex pedicle valve averaging 74% as long as wide and 46% as deep as long ($\bar{l}$ mm (var l) 4·41 (1·956), $\bar{w}$ mm (var w) 6·00 (3·49), r = 0·931; n = 22. $\bar{l}$ mm (var l) 5·56 (0·736), $\overline{th}$ mm (var th) 1·96 (0·276), r = 0·742; n = 7); brachial valve gently convex, averaging 70% as long as wide and 24% as deep as long ($\bar{l}$ mm (var l) 3·67 (0·894), $\bar{w}$ mm (var w) 5·18 (1·395), r = 0·916; n = 21. $\bar{l}$ mm (var l) 4·58 (0·564), $\overline{th}$ mm (var th) 1·11 (0·036), r = 0·829; n = 9); lateral margins of both valves gently rounded, subparallel, anterior margins smoothly rounded or slightly truncated; external surfaces ornamented by 15–19 prominent angular ribs in 2, 9, 6, 6 and 2 brachial valves greater than 3 mm in length, with an average mean wavelength (and variance) of 0·96 mm (0·02) at 5 mm anteromedially of ventral umbones of 11 specimens; brachial valve with shallow, rounded sulcus, narrow posteriorly but becoming broader anteriorly and incorporating 3–6 ribs in 2, 12, 5 and 2 valves respectively; ventral interarea triangular, curved, apsacline, with open delthyrium, dorsal interarea narrow, anacline.

Ventral interior with flattened triangular teeth extending anteriorly on average for 18% of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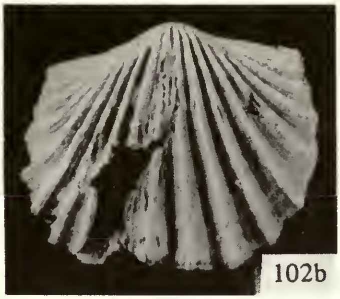
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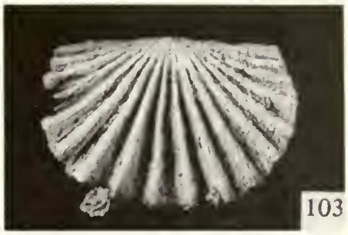
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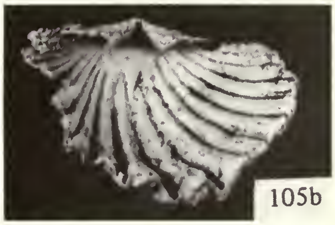
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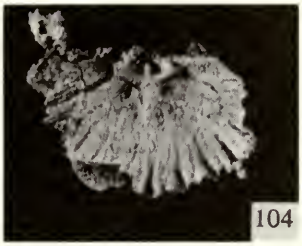
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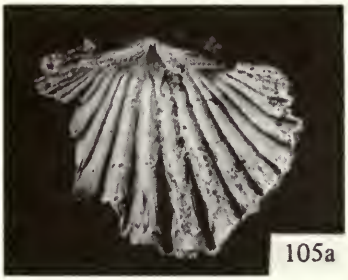
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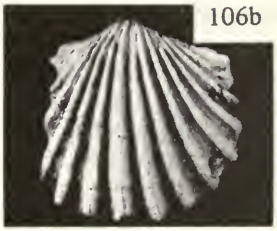
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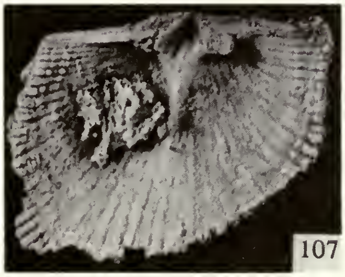
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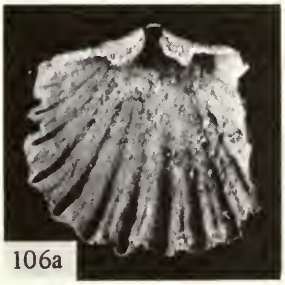
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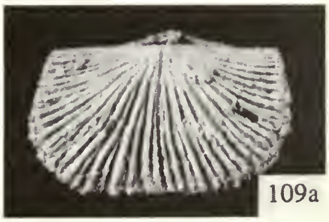
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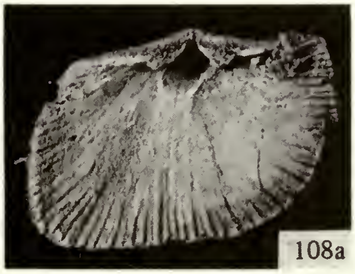
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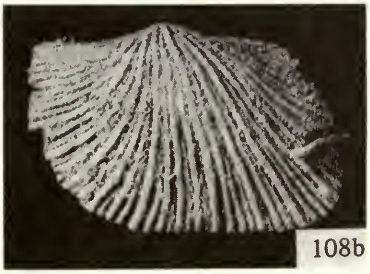
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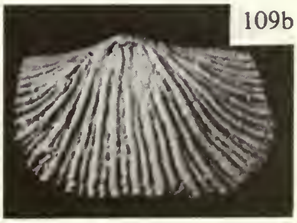

109b

Figs 102–106 *Orthambonites* cf. *panderiana* (Hall & Clarke). Fig. 102a, b, BB 95372, dorsal and ventral views of conjoined valves, both ×5; Fig. 103, BB 95382, exterior of brachial valve, ×5; Fig. 104, BB 95373, interior of incomplete brachial valve, ×5; Fig. 105a, b, BB 95374, interior and oblique anterior view of incomplete pedicle valve, both ×5; Fig. 106a, b, BB 95450, interior and exterior of incomplete pedicle valve: a, ×6; b, ×5.

Figs 107–109 *Taphrorthis immatura* sp. nov. Fig. 107, **holotype** BB 95470, interior of incomplete brachial valve, ×7; Fig. 108a, b, paratype BB 95471, interior and exterior of pedicle valve, both ×6; Fig. 109a, b, paratype BB 95472, dorsal and ventral views of conjoined valves, both ×6.

valve length ($\bar{l}$ mm (var l) 5·25 (0·717), $\bar{l}_{te}$ mm (var l_{te}) 0·93 (0·042), r = 0·767; n = 11), and supported by short, curved, receding, divergent dental plates; floor of pedicle valve with poorly-defined tripartite muscle attachment scars averaging 74% as wide as long ($\bar{l}_{sc}$ mm (var l_{sc}) 1·41 (0·167), $\bar{w}_{sc}$ mm (var w_{sc}) 1·05 (0·046), r = 0·908; n = 8), composed of elongate median adductor scar extending anteriorly beyond anterior margin of flanking elongate diductor scars or slightly elevated tongue-shaped platform.

Dorsal interior with ridge-like cardinal process, oblique sockets, and short, blunt, rod-like, divergent brachiophores with bases extending anteriorly on average 16% of brachial valve length ($\bar{l}$ mm (var l) 4·66 (0·621), $\bar{l}_b$ mm (var l_b) 0·74 (0·017), r = 0·636; n = 11) and 44% as long as the lateral extension of the sockets ($\bar{l}_b$ mm (var l_b) 0·74 (0·017), $\bar{w}_{so}$ mm (var w_{so}) 1·57 (0·080), r = 0·747; n = 11).

		length	width (mm)
Figured material.	Conjoined valves; BB 95372a, b	6·4	7·8
	Incomplete pedicle valve; BB 95374	–	–
	Incomplete pedicle valve; BB 95450	5·0	–
	Brachial valve; BB 95382	4·5	6·6
	Incomplete brachial valve; BB 95373	–	–

All Loc. 1.

Discussion. Despite its cosmopolitan distribution throughout much of the Ordovician, *Orthambonites* displays a strong morphological conservatism, with many species virtually indistinguishable in terms of shell shape and proportions, and morphology of cardinalia. Only the maximum number of ribs developed in adult shells varies sufficiently to provide a ready means of distinguishing between different stocks of *Orthambonites*. In this respect the modal count of 16 ribs for the Tourmakeady specimens greatly restricts the number of species with which the Irish stock can be compared. Thereafter, the highly distinctive form of the ventral muscle field indicates a close morphological affinity with *O. panderiana* from Lower Ordovician successions in Quebec (see Ulrich & Cooper 1938: 102; the species was renamed by Hall & Clarke, 1892: footnote to description of pl. 5). The ventral muscle field of most *Orthambonites* is bilobed. That of *O. panderiana* (Ulrich & Cooper 1938: pl. 15A, fig. 3) is tripartite with an elongate median adductor scar extending anteriorly of the flanking diductors, and in every particular is identical with the muscle field of the Irish *Orthambonites*.

Genus *TAPHRORTHIS* Cooper, 1956

Taphrorthis immatura sp. nov.

Figs 107–109

Diagnosis. Medium-sized, subquadrate to transversely ovate or subcircular *Taphrorthis*, with a moderately to strongly convex pedicle valve averaging 69% as long as wide and 29% as deep as long, and a gently convex brachial valve averaging 65% as long as wide and 23% as deep as long; external ornamentation costellate, with 5–6 narrowly rounded ribs per mm at 2 mm anteromedially of dorsal umbo; ventral muscle field elongately oval, averaging 60% as wide as long.

Name. 'Under-developed'.

Description. Medium-sized, subquadrate to transversely ovate or subcircular, ventribiconvex *Taphrorthis*; pedicle valve moderately to strongly convex, averaging 69% as long as wide (range 63–80%; n = 3) and 29% as deep as long (range 25–31%; n = 3); brachial valve gently convex, averaging 65% as long as wide (range 62–69%; n = 3) and with a maximum thickness developed at sulcate anterior margin averaging 23% of valve length (range 23–24%; n = 3); lateral margins of both valves strongly and smoothly rounded, anterior margin gently rounded with slight median emargination corresponding to brachial sulcus;

external ornamentation costellate with 5–6 narrowly rounded ribs per mm at 2 mm anteromedially of 3 and 1 brachial valves respectively, secondary costellae inserted in 3 generations; brachial valve with broad, shallow, rounded, sulcus; ventral interarea narrow, triangular, curved, apsacline, with open delthyrium, dorsal interarea very narrow, anacline.

Ventral interior with small, thickened, triangular teeth extending anteriorly for 20% of valve length in one specimen, and supported by strong, thickened, subparallel, dental plates with well-developed crural fossettes; floor of pedicle valve with elongately oval muscle platform with smoothly rounded, elevated, anterior rim, averaging 60% as wide as long (range 56–65%; n = 3) and extending anteriorly for 35% and 33% of the length of two valves, muscle platform with poorly-developed median depression extending forward as a slightly elevated, smoothly rounded, medially depressed ridge running for 54% and 42% of the length of two adult valves.

Dorsal interior with short, thickened, spatulate, divergent brachiophores extending anteriorly for an average of 16% of valve length (range 13–20%; n = 3), and flanked laterally by narrowly triangular, deeply incised sockets; notothyrial platform narrowly to broadly triangular, defined anteriorly by elevated, slightly curved margin and averaging 91% as long as wide (range 75–100%; n = 3); cardinal process indistinct or as short, narrow ridge developed posteriorly on notothyrial platform; notothyrial platform buttressed medially by short, rounded ridge extending anteriorly for an average of 58% of valve length (range 54–64%; n = 3).

HOLOTYPE. Incomplete brachial valve; BB 95470. Fig. 107.

		length	width (mm)
PARATYPES.	Conjoined valves; BB 95472a, b	3·6	5·7
	Pedicle valve; BB 95471	5·1	7·8
	Incomplete pedicle valve; BB 95473	–	–
	Brachial valve; BB 95474	4·7	7·4

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. *Taphrorthis* is rare in the Tourmakeady Limestone, and a high proportion of the recovered specimens have been deformed. As a result detailed measurements of shell parameters are unavailable, but there are sufficient data from the few complete, undeformed, specimens to allow comparison with previously-described species of the genus. In the original diagnosis of the genus, Cooper (1956: 326) stated that *Taphrorthis* is characterized by the presence of a cardinal process, albeit one which was often poorly developed. In contrast, two of the three brachial valves in the Tourmakeady sample bore no discernible cardinal process, although the third did possess a short structure consistent with Cooper's description of a 'low inconspicuous ridge'. On balance, the fact that an undifferentiated cardinal process is not discernible in the majority of brachial valves cannot be considered sufficient to justify the exclusion of the sample from *Taphrorthis*. In all other respects the sample conforms to Cooper's diagnosis for the genus, and the Irish species being significantly older than other species so far assigned to the genus suggests that the poor development of the cardinal process is a primitive feature.

The sporadic development of an undifferentiated cardinal process is not the only distinguishing feature of the Irish *Taphrorthis* calling for its specific recognition. The main features characterizing described species of *Taphrorthis* are the shape of the ventral muscle scar and the details of the external ornamentation. In these respects the presence of an elongately ovate ventral platform with a poorly-developed median depression and a relatively fine ornamentation further distinguish the Irish specimens. *T. emarginata* Cooper (1956: 327), the type species of the genus from the Middle Ordovician of Alabama and Tennessee, has a prominent median ridge bisecting the ventral muscle platform and 10 ribs per 5 mm anteromedially; the comparable figure for *T. immatura* is 20–21 ribs per 5 mm. In addition figured specimens of *T. emarginata* display a cardinal process running the entire length of the notothyrial platform; when developed in *T. immatura*, the cardinal process is only discernible at the posterior margin of the notothyrial platform. *T. peculiaris* Cooper (1956: 328), also from the Middle Ordovician of North America, can again be distinguished from the new species by its anteriorly bilobed ventral muscle paltform and coarser ornamentation numbering 12 ribs per 5 mm anteromedially.

Taphrorthis has also been recorded previously from Britain, but comparisons based primarily on the shape of the ventral muscle field and on the external ornamentation confirm the distinctiveness of the new species. Thus the ventral muscle field of *T. aspera* Williams (1962: 102), from the Caradoc of the Girvan District, is strongly trilobed anteriorly and has about 10 ribs per 5 mm anteromedially. Similarly *T. bellatrix* (Reed), also from the Caradoc of the Girvan District (Williams 1962: 103), is readily distinguishable from *T. immatura* by its readily discernible cardinal process, its medially divided ventral muscle field, and its coarser ornamentation, with 10 ribs per 5 mm anteromedially, which bears radial striae and is crossed by concentric lamellae.

Family **DOLERORTHIDAE** Öpik, 1934

Subfamily **GLYPTORTHINAE** Schuchert & Cooper, 1931

Genus ***LOMATORTHIS*** nov.

Diagnosis. Large, biconvex, semicircular to subquadrate glyptorthine with flattened or gently resupinate lateral and anterior margins; external ornamentation costellate, crossed by well-developed concentric growth-lines becoming strongly lamellose peripherally and elevated above shell surface as erect frills; ventral interarea gently curved, apsacline, with narrowly triangular, open delthyrium; dorsal interarea narrow, triangular, anacline, notothyrium open.

Ventral interior with small, triangular, teeth supported by short, receding, divergent dental plates; adductor muscle scars elevated on triangular, posteriorly-tapering, platform, flanked posterolaterally by elongate, concave, diductor muscle scars impressed on valve floor and constrained laterally by dental plates; ventral mantle canal system saccate (?).

Dorsal interior with short, blade-like divergent brachiophores flanking undifferentiated notothyrial platform; adductor scars quadripartite, mantle canal system possibly digitate.

Name. Greek, λῶμα, the hem of a garment.

Type species. *Lomatorthis mimula* sp. nov., from the Tourmakeady Limestone, Co. Mayo.

Discussion. The combination of well-developed dorsal and ventral interareas, open delthyrium and notothyrium, and strong concentric lamellar ornamentation establishes *Lomatorthis* as a representative of the Glyptorthinae. Of those genera presently assigned to that subfamily, the majority can readily be distinguished from the new genus because they possess a prominent cardinal process (e.g. *Glyptorthis* Foerste; *Ptychopleurella* Schuchert & Cooper). In addition, both *Glyptorthis* and *Ptychopleurella* differ in being strongly sulcate, while *Eridorthis* Foerste is uniplicate. *Spinorthis* Wright also possesses a well-developed cardinal process, and can further be distinguished from the new genus by the presence of spinose extensions along the external concentric lamellae.

Among described glyptorthins, *Lomatorthis* is closest to *Lepidorthis* Wang, especially in external form; but there are significant differences internally, especially in the morphology of the cardinalia and disposition of ventral muscle scars, which confirm the distinction between the two genera. In the original diagnosis, *Lepidorthis* is described as lacking a cardinal process (Wang 1955: 330). However, illustrations of the type material reveal a low, rounded, median ridge in the floor of the notothyrial cavity of both brachial valves figured, which is undoubtedly an undifferentiated cardinal process. Such a feature is not evident in any of the Tourmakeady specimens. Moreover, the dorsal interarea of *Lepidorthis* is much narrower than that of *Lomatorthis*, and the dental plates are proportionately much larger. Furthermore, the brachiophores in *Lepidorthis* are strongly thickened, massive, and curved; in

Lomatorthis they are small, delicate and straight. The pattern of muscle attachment in the pedicle valve especially distinguishes the two genera. In *Lepidorthis* the ventral muscle field is undifferentiated and confined to the posterior slope of the median callus. In *Lomatorthis*, the comparable region represents the site of adductor muscle attachment, and is clearly differentiated in all specimens from the flanking, elongate diductor scars.

The distinctive association of morphological features diagnostic of *Lomatorthis* has not been recorded previously in the literature, and for the present the Tourmakeady species remains the sole representative of the new genus.

Lomatorthis mimula sp. nov.

Figs 110–116

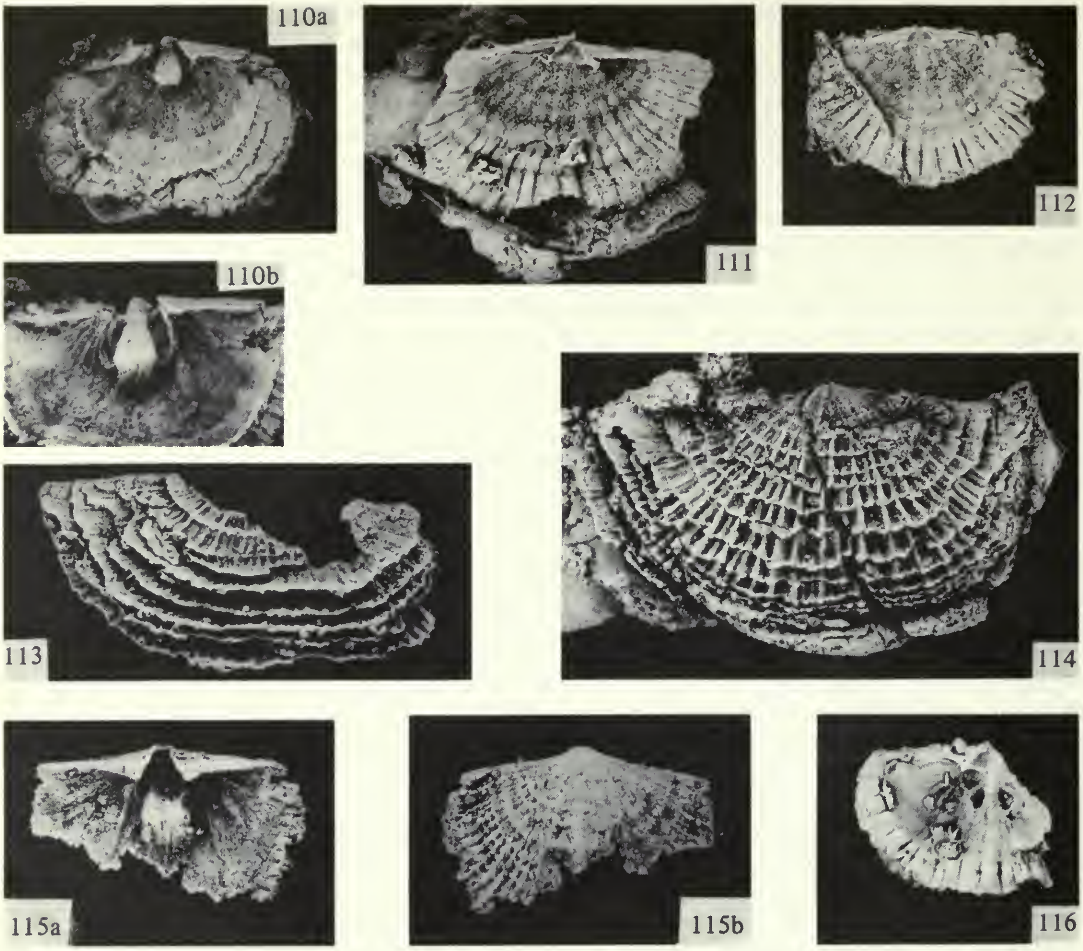
Diagnosis. Large, thick-shelled, semicircular to subquadrate *Lomatorthis*, on average 55% as long as wide; external ornamentation of approximately 10 rounded costellae in a 5 mm sector 5 mm anteromedially of umbo, crossed by strong lamellose concentric growth-lines elevated into erect frills extending up to 0·7 mm above valve surface.

Name. 'Child actress'.

Description. Large, thick-shelled, semicircular to subquadrate *Lomatorthis*, on average 55% as long as wide ($\bar{l}$ mm (var l) 4·3 (3·21), $\bar{w}$ mm (var w) 7·89 (9·41), $r = 0{\cdot}933$; $n = 41$) and attaining a maximum width of 22 mm, both valves strongly to moderately convex, on average 29% as deep as wide (range 28–30% in 3 specimens), with flattened or gently resupinate submarginal platform along smoothly rounded, rectimarginate, anterior and lateral margins; external radial ornamentation costellate, with on average 10 (range 7–12) rounded ribs in a 5 mm sector at 5 mm anteromedially of umbo, with new ribs developed by intercalation when wavelength of existing ribs exceeds 0·6 mm; concentric growth-lines well developed, becoming strongly lamellose peripherally and elevated into erect, concentric frills extending at least 0·7 mm above valve surface; triangular ventral interarea gently curved, apsacline, grooved by well-developed growth-lines, delthyrium large, triangular, open, on average 85% (range 79–93%) as wide as long in 4 specimens; dorsal interarea anacline, narrowly triangular, with broad, triangular, open notothyrium.

Ventral interior with small, flattened, triangular teeth supported by posteriorly tapering, short, receding, divergent dental plates; adductor muscle scars elevated on prominent platform of variable proportions but posteriorly tapering and averaging 89% as wide as long in 4 specimens (range 80–100%), with a maximum elevation, developed anteriorly, on average 63% as high as long (range 52–80%) in 4 specimens, posterior slope of platform marked by anteriorly convex growth-lines; adductor platform flanked laterally by elongate, concave, diductor scars, on average 35% as wide as long in 3 specimens (range 29–40%), defined posterolaterally by inner wall of dental plates, and with slightly elevated, strongly convex, anterior margin extending anteriorly on average 71% of the length of adductor platform (range 66–80%); ventral mantle canal system saccate (?), with two narrow branches of *vascula media* faintly impressed immediately anteriorly of platform but dying out anteriorly, and up to four narrow canals of *vascula genitalia* impressed posterolaterally of adductor platform and dying out peripherally.

Dorsal interior with triangular, gently concave, undivided notothyrial platform, on average 62% as long as wide in 3 specimens (range 47–65%); brachiophores short, simple, divergent, blade-like, lying within plane of dorsal interarea, extending forward for an average of 13% (range 13–14%) of the length of 3 brachial valves, and posterolaterally defining small, triangular, sockets; two pairs of ovate adductor scars strongly impressed immediately anterior of notothyrial cavity symmetrically on either side of short, low median ridge, posterior pair transversely oval in outline, with long axis diverging anteriorly at 70° to median axis of valve, and measuring 1 × 0·5 mm in one valve, anterior pair of adductor scars subparallel with median axis of valve, and measuring 1·4 × 0·9 mm in one valve; 3–4 short



Figs 110–116 *Lomatorthis mimula* gen. et sp. nov. Fig. 110a, b, **holotype** BB 95360, interior and oblique anterior views of incomplete pedicle valve: a, ×2; b, ×3; Fig. 111, paratype BB 95366, interior of incomplete brachial valve, ×4; Fig. 112, paratype BB 95364, interior of brachial valve, ×3; Fig. 113, paratype BB 95361, exterior of incomplete brachial valve, ×3; Fig. 114, paratype BB 95362, exterior of brachial valve, ×3; Fig. 115a, b, paratype BB 95365, interior and exterior of incomplete pedicle valve, ×3; Fig. 116, paratype BB 95363, interior of incomplete brachial valve, ×3.

branches of dorsal mantle canal system of possibly digitate pattern impressed posterolaterally of adductor scars but dying out laterally.

Holotype. Incomplete pedicle valve; BB 95360. Fig. 110.

		length	width (mm)
Paratypes.	Incomplete pedicle valve; BB 95365	–	–
	Brachial valve; BB 95362	11·0	19·8
	Brachial valve; BB 95364	8·0	10·8
	Incomplete brachial valve; BB 95361	–	–
	Incomplete brachial valve; BB 95363	6·6	–
	Incomplete brachial valve; BB 95366	–	–

Type horizon and locality. Loc. 1.

Family **FINKELNBURGIIDAE** Schuchert & Cooper, 1931

Genus ***NOTOSCAPHIDIA*** nov.

Diagnosis. Small, moderately to strongly transversely oval finkelnburgiid, pedicle valve strongly convex with prominent, tapering umbo, brachial valve strongly convex posteromedially, becoming gently convex peripherally; external ornamentation coarsely costellate; ventral interarea broad, gently curved, apsacline, with open delthyrium; dorsal interarea narrowly triangular, anacline, notothyrium open.

Ventral interior with small triangular teeth supported by short, receding, slightly divergent, dental plates forming lateral margins of transversely ovate pseudospondylium, predominantly sessile but becoming free along anterior and anterolateral margins; ventral mantle canal impressions unknown.

Dorsal interior with short, erect brachiophores flanked laterally by deeply incised sockets defined by fulcral plates, and supported by strong, inclined, anteriorly rounded brachiophore bases discrete in juvenile specimens but converging medially in later growth stages to form broadly triangular notothyrial platform with bilobed anterior margin; dorsal adductor muscle scars quadripartite, strongly impressed symmetrically on either side of median ridge; mantle canal system in dorsal valve unknown.

Name. Greek, *νῶτος*, the back, + *σκαφίδιον*, a small boat.

Type species. *Notoscaphidia revelata* sp. nov., from the Tourmakeady Limestone, Co. Mayo.

Discussion. The combination of a ventral pseudospondylium and short, erect brachiophores flanked by fulcral plates and supported by well-developed inclined brachiophore bases establishes *Notoscaphidia* as a representative of the Finkelnburgiidae. The most distinctive feature of the new genus, which immediately distinguishes it from all other finkelnburgiid genera, is the form of the dorsal cardinalia. Although the earliest growth stages have not been recovered, the Tourmakeady residues contained a sufficient size-range of specimens to allow the growth pattern of the cardinalia to be determined in at least the later stages. In the smallest brachial valve available, slightly less than 2 mm in length, the brachiophores are well-developed and are flanked by deeply incised sockets defined by fulcral plates which are only barely elevated above the valve floor. Laterally the brachiophores are supported by well-developed, anteriorly rounded, brachiophore bases which slope down to the valve floor at a low angle and unite with the posterior regions of the median ridge which is well-developed in even the smallest specimens examined. Subsequent growth results in the thickening and elevation of the fulcral plates above the valve floor, and the coalescence of the brachiophore bases to form a strongly concave, anteriorly bilobed, notothyrial platform with a more or less well defined median suture.

In contrast, the notothyrial platform in other finkelnburgiid genera, such a *Finkelnburgia* Walcott and *Fasciculina* Cooper, shows no signs of anterior bilobation, and has a linear to slightly curvate anterior margin defined by discrete, inclined, brachiophore bases united with the median ridge. In addition both *Finkelnburgia* and *Fasciculina* differ from the new genus in having well-developed cardinal processes. *Fasciculina* also differs in having a coarsely fascicostellate ornamentation. Similarly both *Orusia* Walcott and *Diparelasma* Ulrich & Cooper can readily be distinguished from *Notoscaphidia* on the basis of cardinal morphology, as the brachiophore bases in both genera remain discrete throughout ontogeny. *Orusia* can further be distinguished by the lack of pseudospondylium in the ventral valve.

Although the pattern of cardinalia development in *Notoscaphidia* is diagnostic, familial relationship with the other finkelnburgiids is evident. In all genera assigned to the family the brachiophore bases are either subparallel or convergent, but in any event unite with the valve floor (or median ridge) to form the anterior margin of the notothyrial platform. This arrangement represents the maximum development attained by adults of genera such as *Fasciculina* and *Finkelnburgia*, in which the notothyrial platform remains small throughout ontogeny. The comparable arrangement in *Notoscaphidia* represents an intermediate stage in cardinalia development and the brachiophore bases continue to grow both laterally and anteriorly to form a relatively large notothyrial platform.

In many respects the later stages of cardinalia development in *Notoscaphidia* are identical to those recognized in the skenidiid genus *Protoskenidioides* (Williams 1974: 83). In the latter genus, however, the coalescence of the brachiophore bases was usually accompanied by the development of a prominent cardinal process. Furthermore, despite the similarity in the form of the dorsal cardinalia, all skenidiids, including *Protoskenidioides*, can readily be distinguished from the finkelnburgiids in that they have a free or supported spondylium in the pedicle valve while the latter are characterized by a pseudospondylium (the only exception being *Orusia* which lacks both structures). Nevertheless the similarity in the pattern of development between *Protoskenidioides* and *Notoscaphidia* adds further weight to the suggestion that the finkelnburgiids formed the ancestral stock from which the skenidiids developed (Kozlowski 1929, Williams 1974: 85). *Protoskenidioides* was first described from the Upper Arenig Mytton Flags of Shropshire, and was thought to have been ancestral to the very successful genus *Skenidioides* which survived from the Lower Ordovician to the Upper Silurian (Williams 1974: 85). The discovery of both *Protoskenidioides* and a new finkelnburgiid genus in the Tourmakeady Limestone suggests that the skenidiids developed from an ancestral finkelnburgiid stock in the uppermost Cambrian or lowermost Ordovician. The derived skenidiids, the evolution of which was characterized primarily by the development of a spondylium, survived until the Devonian. The ancestral finkelnburgiids, in contrast, never developed a spondylium, and became extinct in the Middle Ordovician.

At present *Notoscaphidia revelata* is the sole known representative of the genus.

Notoscaphidia revelata sp. nov.

Figs 117–123

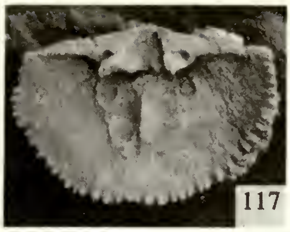
Diagnosis. Small, moderately to strongly transversely oval *Notoscaphidia* with a pedicle valve averaging 71% as long as wide and 46% as deep as long, and a brachial valve averaging 65% as long as wide and 40% as deep as long; external ornamentation coarsely costellate with an average of 6 ribs per mm at 2 mm anteromedially of dorsal umbo.

Name. 'Uncovered'.

Description. Small, moderately to strongly transversely oval *Notoscaphidia*; strongly convex pedicle valve averaging 71% as long as wide ($\bar{l}$ mm (var l) 2·63 (0·056), $\bar{w}$ mm (var w) 3·71 (0·233), r = 0·845; n = 8) and with a maximum thickness averaging 46% of valve length developed posteriorly at prominent, tapering, umbo ($\bar{l}$ mm (var l) 2·63 (0·056), $\overline{th}$ mm (var th) 1·20 (0·023), r = 0·796; n = 8); brachial valve strongly convex posteromedially becoming gently convex peripherally and averaging 65% as long as wide ($\bar{l}$ mm (var l) 2·54 (0·172), $\bar{w}$ mm (var w) 3·88 (0·086), r = 0·747; n = 10) and with a maximum thickness developed at sulcate anterior margin averaging 40% of valve length ($\bar{l}$ mm (var l) 2·61 (0·183), $\overline{th}$ mm (var th) 1·16 (0·018), r = 0·835; n = 10), lateral margins of both valves smoothly rounded, anterior margin with variably gently rounded dorsal sulcus; external ornamentation coarsely costellate with 5–8 rounded ribs per mm at 2 mm anteromedially of the umbones of 2, 7, 2 and 1 brachial valves respectively; ventral interarea broad, apsacline, curved, with open delthyrium, dorsal interarea narrow, curved, anacline.

Ventral interior with small, thickened, triangular teeth supported by short, receding, divergent, dental plates forming lateral margins of anteriorly-rounded, transversely ovate pseudospondylium with free anterior and anterolateral margins and averaging 87% as long as wide ($\bar{l}_p$ mm (var l_p) 0·74 (0·014), $\bar{w}_p$ mm (var w_p) 0·85 (0·009); r = 0·844; n = 8).

Dorsal interior with thickened, erect brachiophores flanked by narrow, deeply incised, triangular sockets defined by well-developed, thickened, fulcral plates; brachiophores



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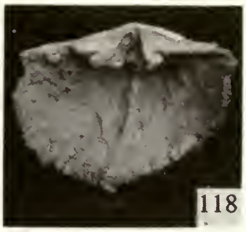

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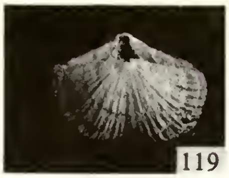

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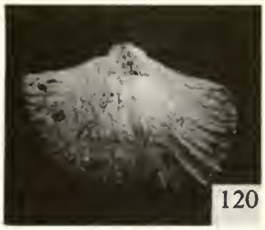

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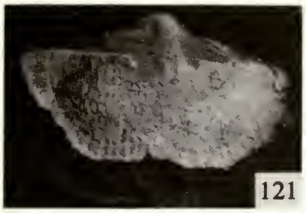

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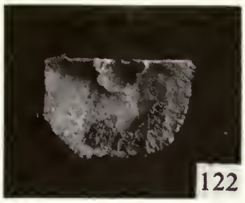

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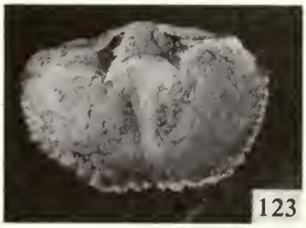

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Figs 117–123 *Notoscaphidia revelata* gen. et sp. nov. Fig. 117, **holotype** BB 95476, interior of brachial valve, ×8; Fig. 118, paratype BB 95484, interior of brachial valve, ×8; Fig. 119, paratype BB 95483, dorsal view of conjoined valves, ×4; Fig. 120, paratype BB 95481, dorsal view of conjoined valves, ×8; Fig. 121, paratype BB 95477, interior of incomplete pedicle valve, ×8; Fig. 122, paratype BB 95480, interior of incomplete pedicle valve, ×4; Fig. 123, paratype BB 95479, interior of brachial valve, ×12.

supported by strong, anteriorly rounded, discrete brachiophore bases united with median ridge in early growth stages but becoming conjoined in adult specimens to form broadly triangular, strongly concave, anteriorly bilobed, notothyrial platform sutured medially and extending anteriorly for an average of 24% of valve length ($\bar{l}$ mm (var l) 2·78 (0·067), $\bar{l}_n$ (var l_n) 0·66 (0·008), r = 0·753; n = 8), and averaging 95% as long as wide ($\bar{l}_n$ mm (var l_n) 0·66 (0·008), $\bar{w}_n$ mm (var w_n) 0·63 (0·005), r = 0·768; n = 9); floor of valve with long, low, rounded, median ridge extending anteriorly from beneath elevated anterior margin of notothyrial platform for an average of 67% of valve length ($\bar{l}$ mm (var l) 2·75 (0·085), $\bar{l}_s$ mm (var l_s) 1·84 (0·086), r = 0·763; n = 10); two pairs of elongately suboval adductor muscle scars impressed strongly on either side of median ridge, and clearly defined by fine elevated rims of shell, posteriormost pair impressed anterolaterally of notothyrial platform with longitudinal axis diverging anteriorly at 60° with median axis of valve and averaging 59% as wide as long (range 50–67%; n = 5); anterior pair impressed anteromedially of posterior pair, flanking, and with longitudinal axis parallel to, median ridge, and averaging 52% as wide as long (range 50–56%; n = 5).

HOLOTYPE. Brachial valve; BB 95476: length 3·0 mm, width 4·6 mm. Fig. 117.

		length	width (mm)
PARATYPES.	Conjoined valves; BB 95478a, b	2·9	3·8
	Conjoined valves; BB 95481a, b	2·6	3·8
	Conjoined valves; BB 95483a, b	2·6	4·0
	Incomplete pedicle valve; BB 95477	–	4·6
	Incomplete pedicle valve; BB 95480	–	–
	Incomplete pedicle valve; BB 95482	–	–
	Brachial valve; BB 95479	1·8	2·8
	Incomplete brachial valve; BB 95484	3·0	–

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. Judged on the statistical analyses of its chief features, *Notoscaphidia revelata* is a morphologically variable species by orthacean standards.

Family **CREMNORTHIDAE** Williams, 1963

Subfamily **PHRAGMORTHINAE** Williams, 1965

Genus ***PHRAGMORTHIS*** Cooper, 1956

Phragmorthis mucronata sp. nov.

Figs 124–129

DIAGNOSIS. Small, ventribiconvex, strongly mucronate *Phragmorthis*; moderately to strongly convex pedicle valve 42% as long as wide and 65% as deep as long; brachial valve moderately convex averaging 49% as long as wide and 36% as deep as long; external ornamentation multicostellate with 6–8 rounded ribs per mm at 1 mm anteromedially of dorsal umbo; dorsal interior with long, low, rounded median septum extending for an average of 81% of valve length.

NAME. 'Sharply pointed'.

DESCRIPTION. Small, ventribiconvex, strongly mucronate *Phragmorthis*; moderately to strongly convex pedicle valve averaging 42% as long as wide ($\bar{l}$ mm (var l) 1·62 (0·082), $\bar{w}$ mm (var w) 3·80 (0·170), r = 0·932; n = 9) and 65% as deep as long ($\bar{l}$ mm (var l) 1·62 (0·082), $\overline{th}$ mm (var th) 1·03 (0·020), r = 0·690; n = 9); brachial valve gently convex averaging 49% as long as wide (range 43–55%; n = 4) and 36% as deep as long (range 31–42%; n = 3); lateral margins of both valves gently rounded, anterior margins strongly rounded, and bilobed by smoothly rounded dorsal median sulcus narrow posteriorly but becoming wider anteriorly; external ornamentation multicostellate with 6–8 rounded ribs per mm at 1 mm anteromedially of the umbones of 6, 2 and 1 brachial valves respectively, new ribs inserted by interior bifurcation of swollen primary costa to give standard ribbing pattern of $1\bar{a}$, 1, $2\bar{a}$, 2, $3\bar{a}$, 3, etc. with $1\bar{a} > 2\bar{a} > 3\bar{a}$; ventral interarea broadly triangular, gently curved, apsacline, with open delthyrium, dorsal interarea narrow, anacline.

Ventral interior with thickened triangular teeth supported by small receding dental plates, posteriorly flanking undifferentiated, elevated, transversely oval muscle attachment platform on average 55% as long as wide ($\bar{l}_{sc}$ mm (var l_{sc}) 0·45 (0·017), $\bar{w}_{sc}$ mm (var w_{sc}) 0·83 (0·036), r = 0·915; n = 8).

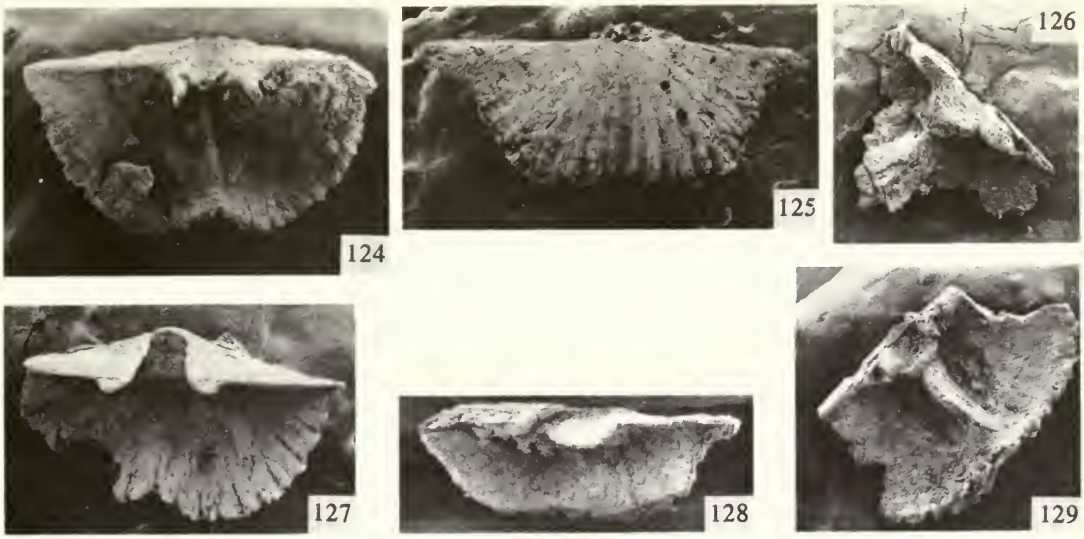
Dorsal interior with long, narrow, suberect, tapering brachiophores, confined to plane of dorsal interarea and extending up to 0·7 mm above valve floor in two specimens, flanked laterally by broad triangular sockets defined anterolaterally by well-developed, elevated, concave, fulcral plates; thickened brachiophore bases unite medially on floor of valve to form elevated, anteriorly tapering, anterior margin of broadly triangular septalium measuring 0·6 × 0·6 mm and 0·5 × 0·5 mm in 2 and 1 brachial valves respectively; floor of valve with long, low, rounded median septum extending anteriorly from anterior margin of septalium for an average of 82% (range 81–84%; n = 3) of valve length; median septum flanked laterally by pair of elongately oval adductor muscle scars with strongly elevated crescentic lateral margins, averaging 50% as wide as long in three specimens (range 44–56%).

HOLOTYPE. Brachial valve; BB 95457: length 2·0 mm, width 3·9 mm. Fig. 124.

		length	width (mm)
PARATYPES.	Conjoined valves; BB 95459a, b	1·9	4·6
	Pedicle valve; BB 95602	1·2	3·3
	Incomplete pedicle valve; BB 95458	–	–
	Incomplete brachial valve; BB 95460	1·9	–
	Incomplete brachial valve; BB 95603	–	–

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. The Tourmakeady residues contained a small number of specimens of a species



Figs 124–129 *Phragmorthis mucronata* sp. nov. Fig. 124, **holotype** BB 95457, interior of brachial valve, ×12; Fig. 125, paratype BB 95459, dorsal view of conjoined valves, ×11; Fig. 126, paratype BB 95603, interior of incomplete brachial valve, ×12; Fig. 127, paratype BB 95458, interior of incomplete pedicle valve, ×12; Fig. 128, paratype BB 95602, interior of pedicle valve, ×12; Fig. 129, paratype BB 95460, interior of incomplete brachial valve, ×12.

reminiscent in external form of some skenidiid genera, but unequivocally assignable to the cremnorthid genus *Phragmorthis* on the basis of its sessile muscle platform in the pedicle valve.

The Irish stock could not readily be confused with any of the few previously-described species of *Phragmorthis*. *P. buttsi* Cooper, the type species, and *P. crassa*, both from the Middle Ordovician of North America (Cooper 1956: 510), are readily distinguishable even in external form, as they have a rounded, non-mucronate outline and are proportionately much more elongate than the Irish representatives. *P. mucronata* is also distinguishable internally in having a much lower median septum and a much more transverse ventral muscle platform.

Family **SKENIDIIDAE** Kozlowski, 1929

Genus ***CROSSISKENIDIUM*** nov.

Diagnosis. Small, moderately to strongly transversely oval skenidiid; pedicle valve moderately convex with prominent rounded umbo; brachial valve shallowly to moderately convex with narrow, smoothly rounded sulcus; external ornamentation finely multicostellate with numerous, closely-spaced, concentric growth-lines elevated as thin peripheral flanges bearing a row of flat, anteriorly rounded, spinose projections; ventral interarea broad, curved, apsacline, with open delthyrium, dorsal interarea narrowly triangular, gently curved, anacline, notothyrium open.

Ventral interior with small triangular teeth supported by short, receding, slightly divergent dental plates forming lateral margins of semicircular spondylium, strongly rounded anteriorly and sessile posteriorly but becoming free anteriorly and anterolaterally; ventral mantle canal system unknown.

Dorsal interior with prominent, erect, tapering brachiophores flanked laterally by shallow sockets defined by thin fulcral plates and supported by strong, thickened, inclined, brachiophore bases sloping down to valve floor to unite with posterior region of long, low, rounded, median ridge; notothyrial platform strongly concave, with tapering triangular anterior margin; adductor muscle scars impressed symmetrically on either side of median ridge as pair of elongately oval areas defined by elevated, smoothly rounded, rim of shell; dorsal mantle canal system unknown.

NAME. Greek, κροσσωτός, fringed.

TYPE SPECIES. *Crossiskenidium spinosum* sp. nov. from the Tourmakeady Limestone, Co. Mayo.

DISCUSSION. The Tourmakeady residues contained a small number of minute brachiopods with an internal morphology indicating skenidiid affinities but with a distinctive external ornamentation not previously recorded in this family. Thus the prominent, erect, brachiophores supported by well-developed, coalescing, brachiophore bases in the brachial valve, combined with a spondylium in the pedicle valve, are diagnostic of the skenidiids. Externally, the spiny lamellose ornamentation of *Crossiskenidium* is so distinctive as to distinguish it immediately from all genera at present assigned to the family.

Crossiskenidium is presently known only from the Tourmakeady Limestone, which also contains a few specimens provisionally identified as a second species of the new genus.

Crossiskenidium spinosum sp. nov.

Figs 130–139

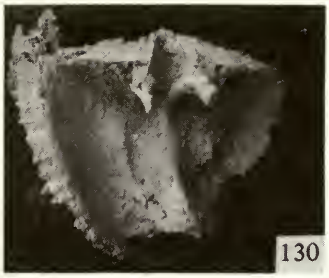
DIAGNOSIS. Small, moderately to strongly oval *Crossiskenidium*; moderately convex pedicle valve averaging 63% as long as wide and 46% as deep as long; shallowly to moderately convex brachial valve averaging 58% as long as wide and 37% as deep as long; external ornamentation finely multicostellate with an average of 10 rounded ribs per mm at 2 mm anteromedially of dorsal umbo crossed by up to 12 closely-spaced, lamellose growth-lines each bearing a row of flat, anteriorly-rounded, peripheral spines.

NAME. 'Spiny'.

DESCRIPTION. Small, moderately to strongly transversely oval *Crossiskenidium*, moderately convex pedicle valve averaging 63% as long as wide (range 57–74%; n = 5) and with a maximum thickness developed at prominent, rounded, ventral umbo averaging 46% of valve length (range 35–52%; n = 5), shallowly to moderately convex brachial valve averaging 58% as long as wide (range 50–74%; n = 5) and with a maximum thickness developed at sulcate anterior margin averaging 37% of valve length (range 28–47%; n = 5); lateral margins of both valves gently convex, anterior margins strongly convex with shallow, rounded, dorsal sulcus with an average width of 0·8 mm at 2 mm anteromedially of the dorsal umbo of 3 valves (range 0·8–0·9 mm); external ornamentation finely multicostellate with an average of 10 (range 10–11; n = 3) rounded ribs per mm at 2 mm anteromedially of dorsal umbo, ribs crossed by closely-spaced, lamellose growth-lines, up to 12 per adult shell, elevated above the valve surface as short flanges extending peripherally as a row of short, flattened, anteriorly-rounded spines.

Ventral interior with small triangular teeth supported by short, receding, divergent dental plates forming lateral margin of anteriorly-rounded, transversely ovate spondylium elevated anteriorly and anterolaterally but sessile posteriorly and extending anteriorly for an average of 33% of valve length (range 30–35%; n = 2) and averaging 73% as long as wide (range 70–78%; n = 3).

Dorsal interior with prominent, erect brachiophores extending for 1·1 mm and 1·2 mm above valve floor in two adult specimens, and flanked by shallow, narrowly triangular sockets defined by thin fulcral plates; brachiophores supported by strong, inclined brachiophore bases united medially with median ridge to define strongly concave, narrowly triangular, notothyrial platform with tapering triangular anterior margin and averaging 79% as wide as long (range 71–83%; n = 3); floor of valve with long, low, rounded median ridge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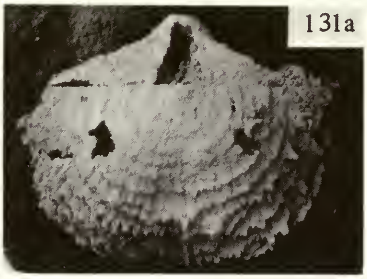
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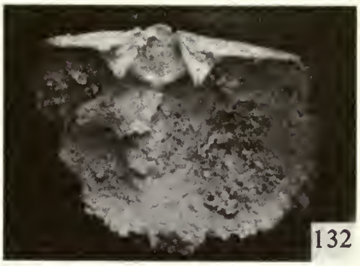
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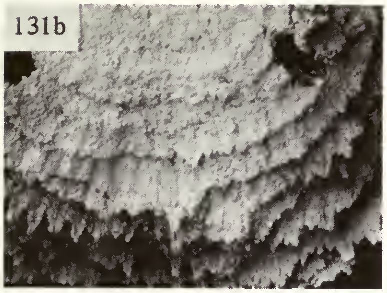
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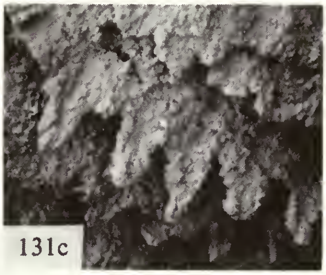
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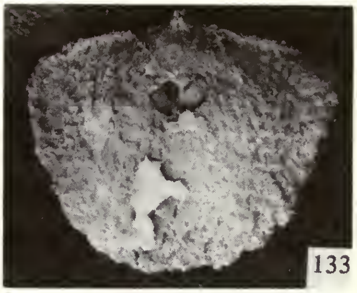
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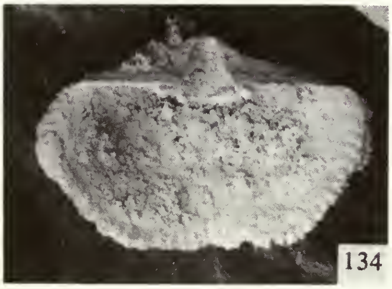
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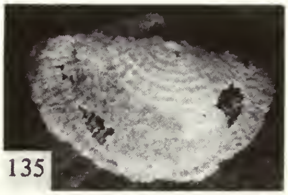
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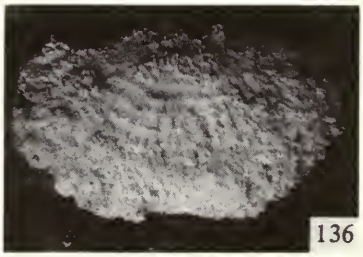
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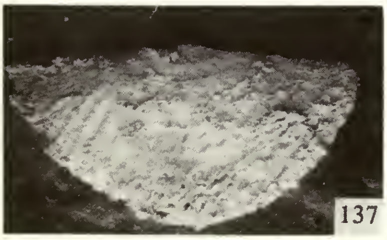
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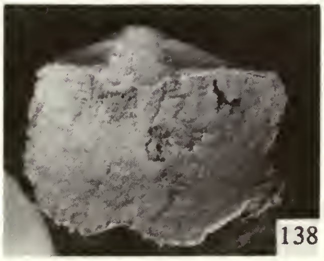
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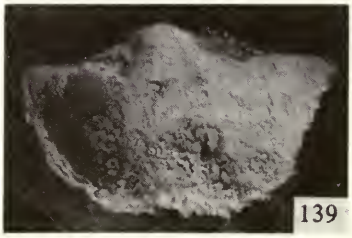
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Figs 130–139 *Crossiskenidium spinosum* gen. et sp. nov. Fig. 130, **holotype** BB 95485, interior of incomplete brachial valve, ×14; Fig. 131a, b, c, paratype BB 95490, dorsal view of conjoined valves: a, ×13; b, detail, ×26; c, detail, ×80; Fig. 132, paratype BB 95494, interior of incomplete brachial valve, ×13; Fig. 133, paratype BB 95491, exterior of incomplete brachial valve, ×18; Fig. 134, paratype BB 95486, interior of pedicle valve, ×12; Fig. 135, paratype BB 95487, dorsal view of conjoined valves, ×8; Fig. 136, paratype BB 95493, dorsal view of conjoined valves, ×10; Fig. 137, paratype BB 95488, exterior of brachial valve, ×13; Fig. 138, paratype BB 95489, interior of incomplete pedicle valve, ×14; Fig. 139, paratype BB 95492, interior of pedicle valve, ×13.

flanked by pair of smoothly rounded, elongately oval muscle scars defined by prominent elevated rim of shell and measuring 0·1 × 0·5 mm in one specimen.

HOLOTYPE. Incomplete brachial valve; BB 95485. Fig. 130.

		length	width (mm)
PARATYPES.	Conjoined valves; BB 95487a, b	2·6	4·2
	Conjoined valves; BB 95490a, b	2·5	3·4
	Conjoined valves; BB 95493a, b	2·6	3·6
	Pedicle valve; BB 95486	2·3	3·5
	Pedicle valve; BB 95492	1·9	3·2
	Incomplete pedicle valve; BB 95489	–	–
	Brachial valve; BB 95488	1·9	3·6
	Brachial valve; BB 95491	2·6	3·3
	Incomplete brachial valve; BB 95494	–	–

TYPE HORIZON AND LOCALITY. Loc 1.

Crossiskenidium*? *lamellosum sp. nov.

Figs 140–146

DIAGNOSIS. Minute, transversely ovate skeniid; moderately convex pedicle valve averaging 51% as long as wide and 56% as deep as long; moderately and smoothly convex brachial valve averaging 44% as long as wide and 62% as deep as long; external ornamentation finely and evenly multicostellate with 15–16 rounded ribs per mm at one mm anteromedially of dorsal umbo, crossed by well-developed lamellose, concentric growth-lines extending as prominent peripheral flanges.

NAME. 'With lamellae'.

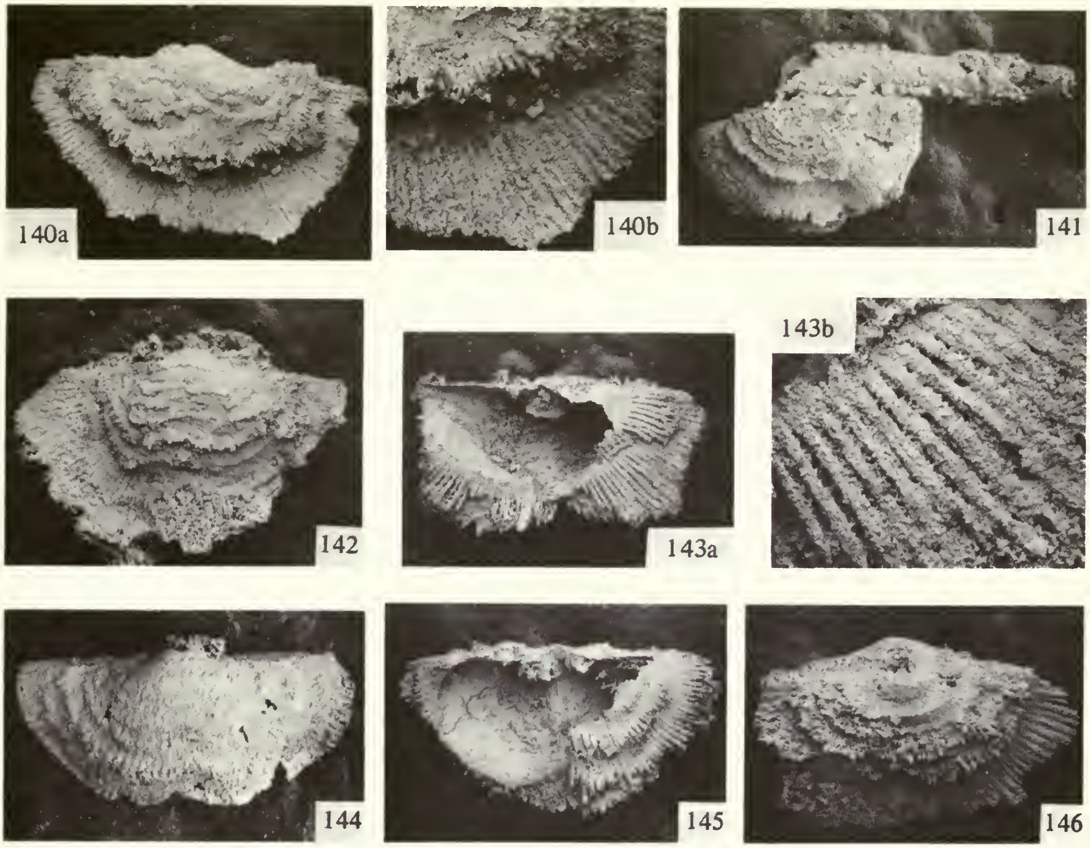
DESCRIPTION. Minute, transversely ovate skenidiids; moderately convex pedicle valve averaging 51% as long as wide (range 46–55%; n = 5) and with a maximum thickness at strongly rounded umbo averaging 56% of valve length (range 47–64%; n = 4); brachial valve moderately and smoothly convex averaging 44% (range 43–45%; n = 2) as long as wide and with a maximum thickness developed at strongly sulcate anterior margin averaging 62% of valve length (range 56–67%; n = 2); lateral margins of both valves smoothly rounded, anterior margin bilobed by prominent, rounded, dorsal median sulcus; external ornamentation finely and evenly multicostellate with 15–16 rounded ribs per mm at one mm anteromedially of the umbones of 2 and 3 brachial valves respectively; ribs crossed by well-developed concentric growth-lines becoming strongly lamellose in adult growth stages and extending peripherally beyond valve margins for up to 0·7 mm as prominent flanges.

Ventral interior with small triangular teeth supported by short, receding, parallel, dental plates forming lateral margin of posteriorly-rounded free spondylium with dimensions of 0·5 × 0·5 mm in one specimen.

Dorsal interior with prominent, erect brachiophores flanked by shallow, triangular, sockets defined by thin fulcral plates and supported by well-developed, inclined, coalescing, brachiophore bases.

HOLOTYPE. Conjoined valves; BB 95495a, b: length 1·5 mm, width 2·8 mm. Fig. 140.

		length	width (mm)
PARATYPES.	Conjoined valves; BB 95498a, b	1·3	2·2
	Conjoined valves; BB 95500a, b	1·0	2·1
	Conjoined valves; BB 95501a, b	1·3	2·1
	Conjoined valves; BB 95616a, b	1·5	2·6
	Pedicle valve; BB 95496	1·5	2·5
	Pedicle valve; BB 95499	1·4	2·8
	Brachial valve; BB 95497	1·7	2·9



Figs 140–146 *Crossiskenidium*? *lamellosum* sp. nov. Fig. 140, **holotype** BB 95495, dorsal view of conjoined valves: a, ×17; b, enlargement of ornamentation, ×35; Fig. 141, paratype BB 95616, dorsal view of conjoined valves attached(?) to hollow tube, ×12; Fig. 142, paratype BB 95501, ventral view of conjoined valves, ×16; Fig. 143a, b, paratype BB 95496, interior of pedicle valve: a, ×11; b, ×44; Fig. 144, paratype BB 95499, exterior of pedicle valve, ×14; Fig. 145, paratype BB 95497, interior of brachial valve, ×13; Fig. 146, paratype BB 95500, dorsal view of conjoined valves, ×20.

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. Apart from representatives of the type species of *Crossiskenidium*, the Tourmakeady residues also yielded a small sample of distinctively ornamented minute brachiopods, which on the available information may be provisionally assigned to the new genus. The sample consists predominantly of conjoined valves, along with a few separated valves which are mostly fragmentary and have much of their internal morphology obscured by siliceous encrustations. However, dissections of some conjoined valves revealed sufficient information on the form of the dorsal cardinalia and the ventral muscle field to demonstrate unequivocally their skenidiid affinities. Thus the presence of a free spondylium in the pedicle valve, and inclined brachiophore bases uniting with the valve floor in the dorsal valve, are diagnostic of this family. Externally, however, the specimens bear lamellae which are proportionately larger than those in *C. spinosum* and which do not bear rows of flat spines along their peripheries. Other features which further justify the erection of at least a new species are the finer radial ornamentation and the development, interiorly, of a free spondylium.

Genus *PROTOSKENIDIOIDES* Williams, 1974

Protoskenidioides hibernicus sp. nov.

Figs 147–152

DIAGNOSIS. Transversely semi-oval mucronate *Protoskenidioides*, with a strongly convex pedicle valve averaging 49% as long as wide and 57% as deep as long, and a gently convex to almost planar brachial valve averaging 50% as long as wide and 59% as deep as long at sharply sulcate anteromedian margin; external ornamentation costate with an average of 14 rounded ribs in adult brachial valves.

NAME. 'Irish'.

DESCRIPTION. Small, transversely semi-oval mucronate *Protoskenidioides* with juvenile specimens flattened, sub-pyramidal; adult pedicle valves strongly convex averaging 49% as long as wide ($\bar{l}$ mm (var l) 1·69 (0·094), $\bar{w}$ mm (var w) 3·47 (0·238), r = 0·747; n = 10) and 57% as deep as long ($\bar{l}$ mm (var l) 1·64 (0·150), $\overline{th}$ mm (var th) 0·93 (0·047), r = 0·932; n = 14); brachial valve gently convex to almost planar, on average 50% as long as wide ($\bar{l}$ mm (var l) 1·60 (0·037), $\bar{w}$ mm (var w) 3·27 (0·160), r = 0·629; n = 10) and with a maximum thickness at sharply sulcate anteromedian margin averaging 59% of valve length ($\bar{l}$ mm (var l) 1·48 (0·037), $\overline{th}$ mm (var th) 0·87 (0·010), r = 0·802; n = 9); lateral margins of both valves smoothly rounded, anterior margins rounded or slightly truncated, commonly bilobed by sharp, narrow, dorsal median sulcus on average 0·48 mm wide (range 0·3–0·6 mm in 7 valves) at one mm anteromedially of dorsal umbo; radial ornamentation costate, with 12–16 ribs on 1, 4, 6, 2 and 1 brachial valves respectively; strong ventral median costa forms carina of pedicle valve complimentary to dorsal sulcus and attains a maximum width of 0·5 mm in 4 adult valves; ventral interarea broad, apsacline, gently curved, with open delthyrium, dorsal interarea narrow, planar, anacline.

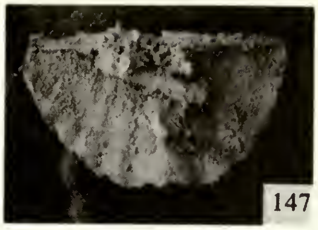
Ventral interior with short, tapering teeth, and shallow, concave, free spondylium, rounded anteriorly, averaging 69% as wide as long ($\bar{l}_{sp}$ mm (var l_{sp}) 0·53 (0·007), $\bar{w}_{sp}$ mm (var w_{sp}) 0·37 (0·007), r = 0·8; n = 6) and extending for an average of 61% of the length of the ventral interarea ($\bar{l}_{sp}$ mm (var l_{sp}) 0·53 (0·013); $\bar{l}_{in}$ mm (var l_{in}) 0·87 (0·017), r = 0·573; n = 9).

Dorsal interior with narrow, subparallel, erect brachiophores flanked by narrow triangular sockets constrained anterolaterally by well-defined fulcral plates, brachiophores extending ventrally up to 0·8 mm above valve floor, supported by strong, curved, brachiophore bases united medially in adult specimens to form elevated bilobed anterior margin of notothyrial platform averaging 88% as long as wide ($\bar{l}_n$ mm (var l_n) 0·48 (0·002), $\bar{w}_n$ mm (var w_n) 0·53 (0·003), r = 0·547; n = 6); faint low rounded cardinal process developed posteromedially on notothyrial platform; floor of brachial valve with long, low, rounded, median septum extending anteriorly for an average of 1·1 mm in 5 adult valves (range 1·1–1·2 mm), anterior margin of median septum abruptly elevated to form prominent erect spine extending up to 0·7 mm above valve floor in adult specimens; adductor muscle field divided by median septum into pair of elongately oval, subparallel, impressions defined anteriorly and laterally by elevated rim, and with dimensions of 0·5 × 0·3 mm in one specimen.

HOLOTYPE. Complete brachial valve; BB 95451: length 1·5 mm, width 2·6 mm. Fig. 147.

		length	width (mm)
PARATYPES.	Conjoined valves; BB 95452a, b	1·8	3·2
	Conjoined valves; BB 95454a, b	1·1	2·6
	Conjoined valves; BB 95456a, b	0·5	2·2
	Incomplete pedicle valve; BB 95453	1·3	–
	Incomplete brachial valve; BB 95455	–	–

TYPE HORIZON AND LOCALITY. Loc. 1.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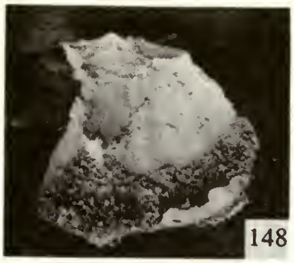
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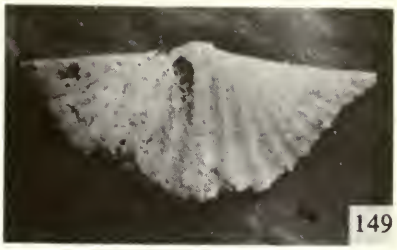
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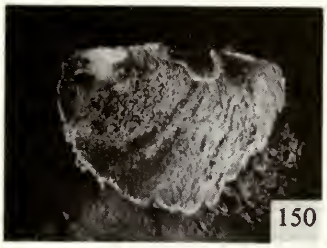
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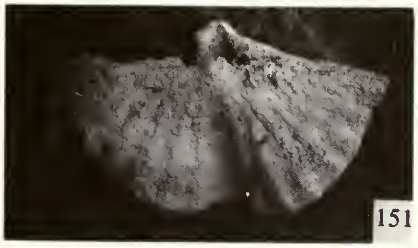
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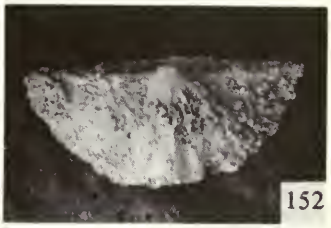
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Figs 147–152 *Protoskenidioides hibernicus* sp. nov. Fig. 147, **holotype** BB 95451, interior of brachial valve, ×14; Fig. 148, paratype BB 95455, interior of incomplete brachial valve, ×16; Fig. 149, paratype BB 95454, ventral view of conjoined valves, ×19; Fig. 150, paratype BB 95453, interior of pedicle valve, ×18; Fig. 151, paratype BB 95452, dorsal view of conjoined valves, ×14; Fig. 152, paratype BB 95456, ventral view of juvenile conjoined valves, ×22.

Discussion. The genus *Protoskenidioides* was erected to incorporate primitive skenidiids characterized by a pattern of cardinalia development which had not previously been recorded in this family (Williams 1974: 83). In juvenile *Protoskenidioides* the brachiophore bases are discrete, but in adult valves subsequently unite medially to form a bilobed notothyrial platform surmounted posteriorly by a narrow ridge-like cardinal process marking the line of suture. Concomitantly the median septum, initially a discrete low narrow ridge situated anteriorly of the brachiophore bases, grows both anteriorly and posteriorly and unites with the anterior margin of the notothyrial platform (Williams 1974: 84). This contrasts with the pattern of cardinalia development in other skenidiids, such as *Skenidioides*, in which the notothyrial platform is evenly convex anteriorly in both juveniles and adults, and shows no signs of having developed from the coalescence of discrete brachiophore bases. The recognition of the *Protoskenidioides*-type of development in the Tourmakeady specimens confirms their assignment to that genus rather than to *Skenidioides*; externally the two genera are very similar in appearance.

The Tourmakeady specimens have many features in common with *P. revelata* (Williams 1974: 85), the type species of the genus from the Arenig of Shropshire. Apart from the similarity in cardinalia development mentioned above, the two stocks are virtually indistinguishable in shell size and proportions and in number of ribs. However, differences which justify the recognition of the Tourmakeady specimens as a new species are discernible, in particular the development of a spinose extension on the median septum and a curved ventral interarea. In addition the proportions of the notothyrial platform readily distinguish the two stocks, being strongly transverse in *P. revelata* (about half as long as wide) as compared with only slightly transverse in the Irish specimens (ranging from 80–100% as long as wide).

Suborder **CLITAMBONITIDINA** Öpik, 1934

Superfamily **CLITAMBONITACEA** Winchell & Schuchert, 1893

Family **POLYTOECHIIDAE** Öpik, 1934

Genus ***ACANTHOTOECHIA*** nov.

DIAGNOSIS. Medium-sized, concavo-convex polytoechiid, subelliptical to semicircular in outline; pedicle valve moderately to strongly convex with prominent, tapering, triangular umbo; brachial valve gently and smoothly concave; external ornamentation unequally parvicostellate, with ribs bearing rows of fine, hollow spines peripherally; ventral interarea broad, planar, apsacline, delthyrium closed dorsally by well-developed, smoothly rounded, strongly convex pseudodeltidium, posteriorly enclosing circular pedicle foramen, dorsal interarea narrow, catacline, notothyrium flanked by weak chilidial plates.

Ventral interior with small, thickened, triangular teeth supported by well-developed, divergent, dental plates defining lateral margins of tripartite ventral muscle field with prominent, elevated median adductor scar callist; ventral mantle canal system unknown.

Dorsal interior with narrow, thickened cardinalia with well-developed, gently curved, socket ridges defining narrow triangular sockets and supported by callus deposits laterally to define narrow notothyrial platform surmounted by thickened, ridge-like, cardinal process; floor of valve with well-defined subperipheral ridge; muscle attachment scars and mantle canal system unknown.

NAME. Greek, ἀκανθώδης, thorny, + τοῖχος, wall.

TYPE SPECIES. *Acanthotoechia hibernica* sp. nov. from the Tourmakeady Limestone, Co. Mayo.

DISCUSSION. A small sample of shells from the Tourmakeady Limestone can confidently be assigned to the Polytoechiidae on the basis of a strong, arched pseudodeltidium and characteristic internal morphology. Their external ornamentation, however, parvicostellate with fine erect spines, has not previously been recorded in any polytoechiid and warrants generic recognition. The majority of polytoechiids are finely multicostellate; and in *Tritoechia* swollen hollow costellae are a conspicuous component of the radial ornamentation but these are never prolonged into spines.

In other respects the new genus appears closest to *Pomatotrema* Ulrich & Cooper, both being distinguished from other described unequally biconvex polytoechiids in their concavo-convex profile. Internally the ventral muscle field and cardinalia of the new genus are also similar to those in *Pomatotrema*. In *Pomatotrema*, however, the dental plates are much more strongly developed and do not recede as in the Irish specimens.

The only species, *Acanthotoechia hibernica*, is at present known only from the Tourmakeady Limestone.

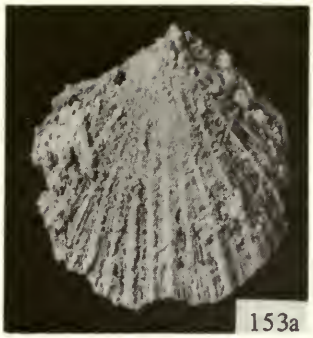
Acanthotoechia hibernica sp. nov.

Figs 153–159

DIAGNOSIS. Medium-sized, subelliptical to semicircular *Acanthotoechia*; pedicle valve averaging 100% as long as wide and 31% as deep as long; brachial valve subquadrate to semicircular averaging 66% as long as wide and 20% as deep as long; external ornamentation unequally parvicostellate with 6 or 7 rounded ribs per mm at 2 mm anteromedially of dorsal umbo, swollen primary ribs bearing two rows of fine cylindrical spines, erect in lateral view but inclined laterally when viewed anteriorly, and with an average diameter of 80 μm, fine intermediary ribs each bearing a single row of hollow erect spines with an average maximum diameter of 60 μm.

NAME. 'Irish'.

DESCRIPTION: Medium-sized, concavo-convex *Acanthotoechia*, subelliptical to semicircular in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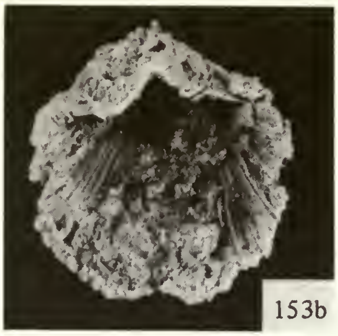
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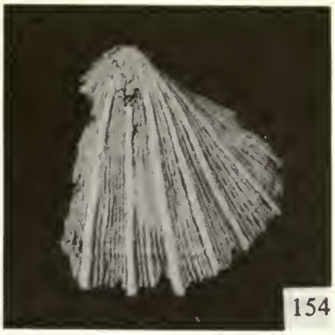
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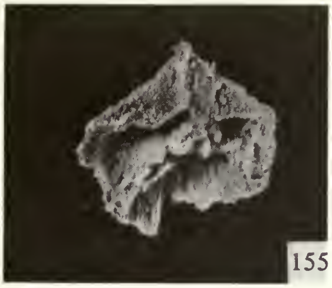
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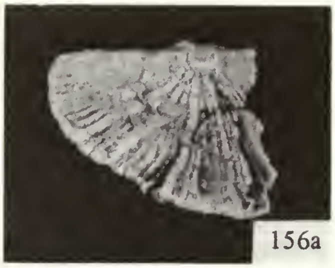
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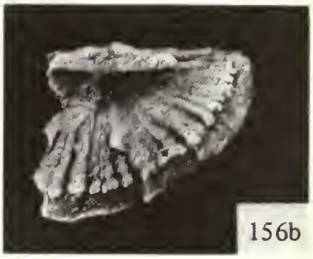
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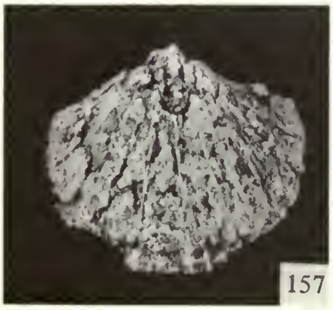
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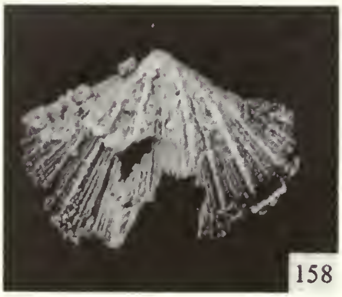
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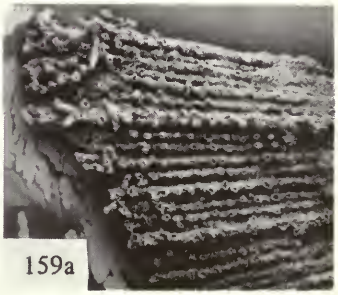
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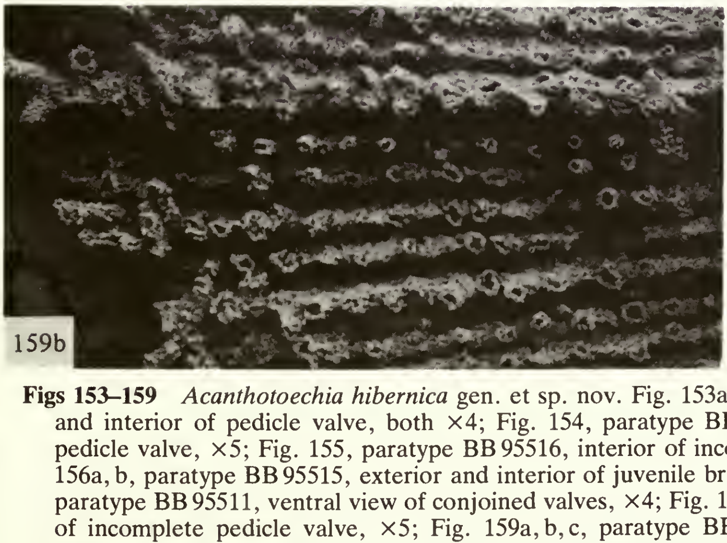
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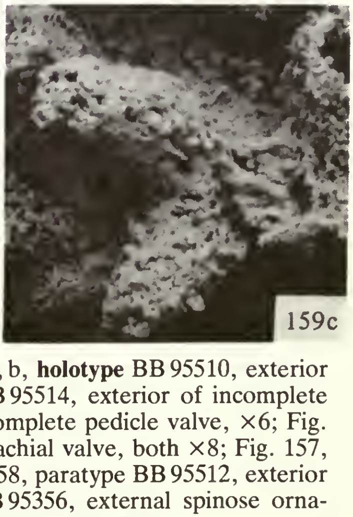
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Figs 153–159 *Acanthotoechia hibernica* gen. et sp. nov. Fig. 153a, b, **holotype** BB 95510, exterior and interior of pedicle valve, both ×4; Fig. 154, paratype BB 95514, exterior of incomplete pedicle valve, ×5; Fig. 155, paratype BB 95516, interior of incomplete pedicle valve, ×6; Fig. 156a, b, paratype BB 95515, exterior and interior of juvenile brachial valve, both ×8; Fig. 157, paratype BB 95511, ventral view of conjoined valves, ×4; Fig. 158, paratype BB 95512, exterior of incomplete pedicle valve, ×5; Fig. 159a, b, c, paratype BB 95356, external spinose ornamentation on fragment: a, ×17; b, ×50; c, twin spines on primary rib, ×200.

outline with prominent, tapering, triangular ventral umbo; pedicle valve moderately to strongly convex averaging 100% as long as wide (ranging from 98% as long as wide to 98% as wide as long in two specimens) and averaging 31% as deep as long (range 25–36%; n = 2); brachial valve gently concave, transversely subquadrate to semicircular, averaging 66% as long as wide (range 65–67%; n = 2) and with a maximum thickness averaging 20% of valve length (range 18–21%; n = 2); lateral and anterior margins of both valves strongly and evenly rounded; external ornamentation unequally parvicostellate with 6 or 7 rounded ribs per mm at 2 mm anteromedially of the umbones of two brachial valves, divided into narrowly triangular sectors by a moderate to strong thickening of every fifth to seventh rib; external surfaces spinose with accentuated primary ribs bearing two rows of fine, cylindrical hollow spines, erect in lateral view but inclined laterally when viewed anteriorly and with an average maximum diameter of 80 μm (range 70–90 μm; n = 12), fine intermediary ribs each bearing a single row of fine, cylindrical, hollow, erect spines with an average maximum diameter of 60 μm (range 50–65 μm; n = 14); ventral interarea broad, triangular, planar, apsacline, delthyrium closed dorsally by well-developed, smoothly rounded, convex pseudodeltidium enclosing posteriorly-situated circular pedicle foramen with a maximum diameter of 0·6 mm in 3 specimens, dorsal interarea very narrow, catacline, notothyrium flanked by weakly-developed chilidial plates.

Ventral interior with small, thickened, triangular teeth supported by well-developed, receding, dental plates forming lateral margins of well-defined, broadly triangular, sessile, ventral muscle field averaging 91% as long as wide (range 87–94%; n = 2), muscle field tripartite with prominent, narrowly triangular, elevated median adductor ridge with a maximum width anteriorly of 0·6 mm in two specimens.

Dorsal interior with narrow, thickened cardinalia with well-developed, gently curved, socket ridges defining narrowly triangular sockets supported by callus deposits laterally to define narrow notothyrial platform surmounted by thickened ridge-like cardinal process.

HOLOTYPE. Pedicle valve; BB 95510: length 9·1 mm, width 8·6 mm. Fig. 153.

		length	width (mm)
PARATYPES.	Conjoined valves; BB 95511a, b	7·7	8·0
	Incomplete pedicle valve; BB 95512	–	8·6
	Incomplete pedicle valve; BB 95514	6·5	–
	Incomplete pedicle valve; BB 95516	–	–
	Incomplete pedicle valve; BB 95356	–	–
	Brachial valve; BB 95513	5·1	7·6
	Incomplete brachial valve; BB 95515	3·1	–

TYPE HORIZON AND LOCALITY. Loc. 1.

Genus *POMATOTREMA* Ulrich & Cooper, 1932

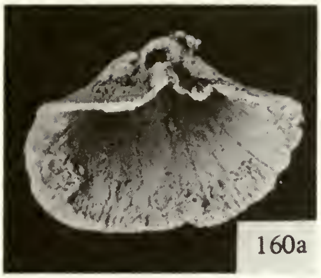
Pomatotrema inconspicuum sp. nov.

Figs 160–162

DIAGNOSIS. Small, biconvex to almost plano-convex *Pomatotrema*, strongly transversely ovate in outline; pedicle valve strongly convex averaging 56% as long as wide and 56% as deep as long with prominent tapering ventral umbo; brachial valve shallowly convex to almost planar, 43% as long as wide and 28% as deep as long; external ornamentation multicostellate with 6–7 ribs per mm at 2 mm anteromedially of dorsal umbo.

NAME. 'Unremarkable'.

DESCRIPTION. Small, biconvex to almost plano-convex *Pomatotrema*, strongly transversely ovate in outline with prominent tapering, triangular, ventral umbo; pedicle valve strongly convex averaging 56% as long as wide (range 52–66%; n = 4) and 56% as deep as long (range 51–60%; n = 4); brachial valve gently convex, especially posteromedially, becoming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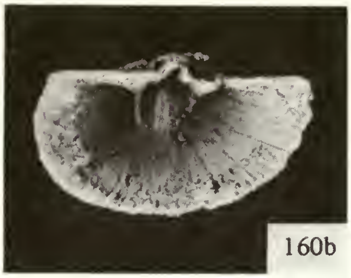
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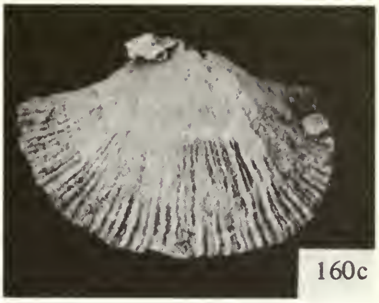
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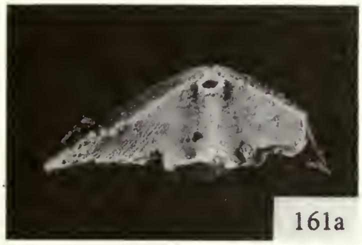
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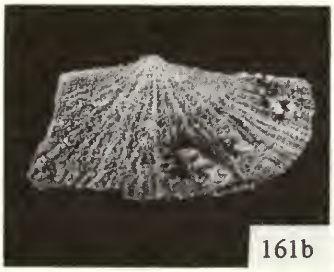
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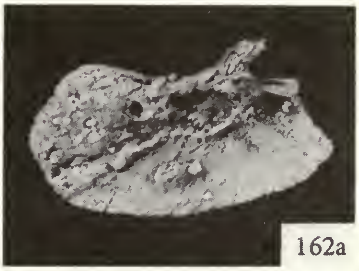
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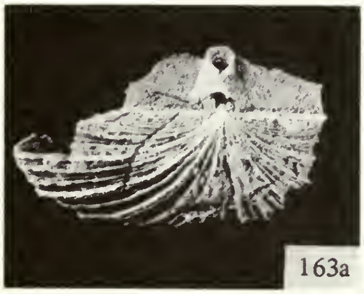
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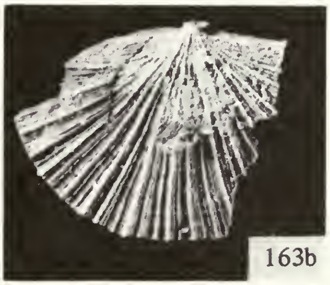
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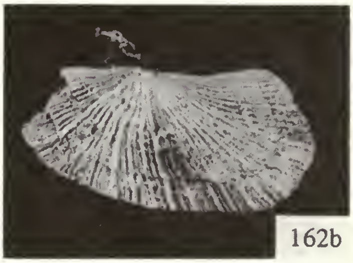
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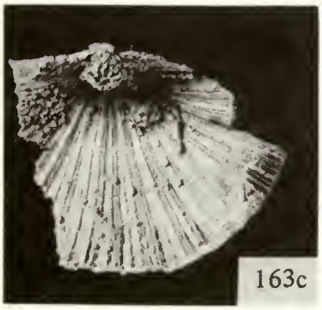
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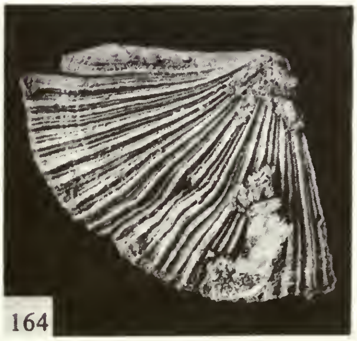
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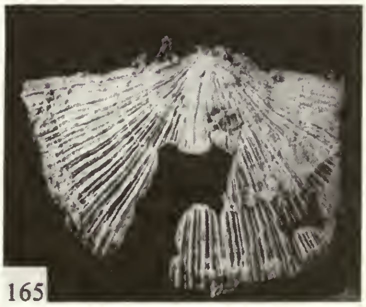
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Figs 160–162 *Pomatotrema inconspicuum* sp. nov. Fig. 160a, b, c, **holotype** BB 95522, pedicle valve: a, interior, ×4; b, inclined anterior view of valve interior, ×4; c, exterior, ×5; Fig. 161a, b, paratype BB 95524, posterior and external views of incomplete pedicle valve: a, ×4; b, ×5; Fig. 162a, b, paratype BB 95525, interior and exterior of brachial valve, both ×5.

Figs 163–165 *Tritoechia* sp. Fig. 163a, b, c, BB 95529, posterior, dorsal and ventral views of incomplete conjoined valves: a, ×4; b, c, both ×3; Fig. 164, BB 95530, exterior of incomplete brachial valve, ×2; Fig. 165, BB 95528, exterior of incomplete brachial valve, ×2.

almost planar anteriorly and anterolaterally, 43% as long as wide in one specimen and attaining a maximum thickness of 28% of valve length posteromedially; lateral margins of both valves strongly rounded, anterior margins gently rounded to almost planar; external ornamentation multicostellate with 6–7 rounded ribs per mm at 2 mm anteromedially of dorsal umbones of two brachial valves; ventral interarea broad, triangular, strongly to moderately apsacline, planar or slightly concave, delthyrium closed dorsally by well-developed, strongly arched pseudodeltidium enclosing posteriorly situated pedicle foramen with a maximum diameter of 0·7 mm in 4 specimens; dorsal interarea narrow, planar, catacline, notothyrium covered by gently arched chilidial plates.

Ventral interior with small, thickened, triangular teeth supported by strongly receding dental plates very faint dorsally but becoming prominent and thickened posteriorly to form lateral margins of well-defined, elongately oval, tripartite ventral muscle field with prominent, elongately oval, rounded, median adductor ridge flanked by narrow, parallel-sided, diductor scars.

Dorsal interior with narrow, thickened cardinalia with well-developed, thickened, rounded, gently curved, socket ridges defining narrow triangular sockets, and united medially to define small triangular notothyrial platform surmounted by thickened, rounded, ridge-like cardinal process; notothyrial platform supported medially to floor of valve by short, rounded, thickened, median ridge.

HOLOTYPE. Pedicle valve; BB 95522: length 5·9 mm, width 8·9 mm. Fig. 160.

PARATYPES. Pedicle valve, BB 95526 (length 3·8 mm, width 7·1 mm); incomplete pedicle valve, BB 95524; incomplete brachial valves BB 95523, 95525 (length 3·5 mm), 95527.

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. The combination of polytoechiid cardinalia, distinctive ventral morphology, almost planar brachial valve, and multicostellate ornamentation confirms the presence of representatives of *Pomatotrema* in the Tourmakeady Limestone.

When compared with other species of *Pomatotrema*, the Irish stock is noticeably more transversely oval, more so even than *P. transversum* Ulrich & Cooper (1938: 174) from the Lower Ordovician Arbuckle Limestone of Oklahoma. The Irish species is further distinguished by the presence of a relatively well-developed, catacline, dorsal umbo. In addition *P. inconspicuum* is smaller than most described species of *Pomatotrema*, but has a proportionately much larger pedicle foramen.

Genus ***TRITOECHIA*** Ulrich & Cooper, 1936

Tritoechia sp.

Figs 163–165

DIAGNOSIS. Large, biconvex, transversely semi-ellipitical *Tritoechia*; pedicle valve moderately curved with a prominent, gently rounded, umbo, about 67% as long as wide and 25% as deep as long; brachial valve moderately convex, about 45% as long as wide and 30% as deep as long; radial ornamentation fascicostellate with 5 or 6 angular ribs per mm at 5 mm anteromedially of dorsal umbo.

DESCRIPTION. Large, biconvex, transversely semi-elliptical *Tritoechia*; pedicle valve moderately convex, attaining an estimated maximum length of 20 mm and about 67% as long as wide and 25% as deep as long, brachial valve moderately convex with minute umbo, estimated to be 45% as long as wide and 30% as deep as long; radial ornamentation fascicostellate with 5 or 6 angular ribs per mm at 5 mm anteromedially of the dorsal umbones of two specimens, ribs hollow, especially in adult growth stages; ventral interarea broad, triangular, planar to slightly concave, moderately apsacline to almost catacline, delthyrium closed by strong arched pseudodeltidium enclosing posteriorly-situated circular pedicle foramen with a diameter of 0·8 mm in one specimen, dorsal interarea very narrow, planar, anacline, notothyrium covered by small chilidial plates.

Ventral interior with small, triangular, thickened teeth supported by strongly receding dental plates forming lateral margins of tripartite ventral muscle field.

Dorsal interior with small thickened cardinalia consisting of socket ridges joined medially by callus deposits.

Figured material. Incomplete conjoined valves, BB 95529a, b (length 8·4 mm); incomplete pedicle valve, BB 95528 (length 19·6 mm); incomplete brachial valve, BB 95530 (length 14·1 mm). All Loc. 1.

Discussion. In addition to the new species of *Pomatotrema* Ulrich & Cooper and *Acanthotoechia* gen. nov., the Tourmakeady Limestone yielded a small number of incomplete specimens clearly belonging to a third polytoechiid genus. The specimens are distinguished from the other two genera by being much larger and more strongly biconvex, and by having a distinctive fascicostellate ornamentation of hollow, angular, ribs. These features suggest an affinity with *Tritoechia* Ulrich & Cooper. Certainly those aspects of internal morphology which can be determined in the sparse, partially preserved Irish specimens support this belief.

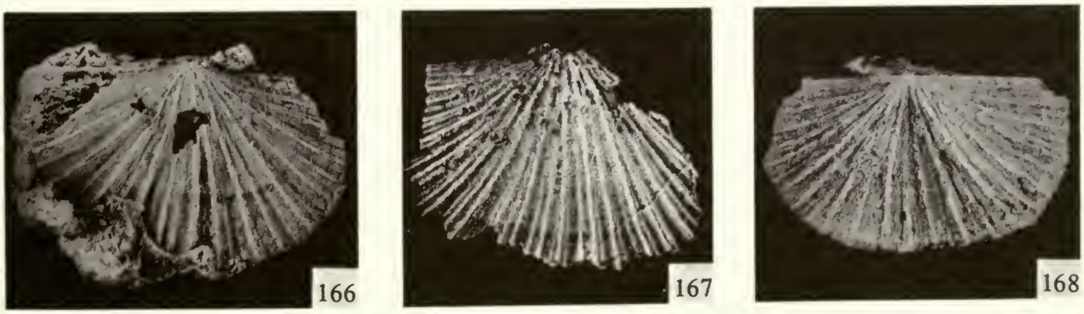
The size and external morphology of the Irish specimens are reminiscent of *T. occidentalis* Ulrich & Cooper (1938: 164) from the Lower Ordovician Sarbach Formation of Canada. However, the former can readily be distinguished by their fascicostellate ornamentation and considerably more transverse outline. In view of the lack of detailed information on internal morphology, no meaningful comparison between the Irish stock and its assumed congeneric species is possible, and specific recognition is withheld.

Superfamily indet.

Orthidina gen. et sp. indet.

Figs 166–168

A small number of specimens from the Tourmakeady residues (BB 95588–92) cannot be identified generically because their internal morphology is indeterminable. The specimens are ventribiconvex, transversely subquadrate to semicircular in outline, and have a fascicostellate ornamentation. The delthyrium and notothyrium appear to be open, which suggests that the specimens are orthaceans.



Figs 166–168 Orthidina, gen. et sp. indet. Fig. 166, BB 95588, ventral view of conjoined valves, ×4; Fig. 167, BB 95590, exterior of pedicle valve, ×4; Fig. 168, BB 95589, exterior of brachial valve, ×4.

Order **STROPHOMENIDA** Öpik, 1934

Suborder **STROPHOMENIDINA** Öpik, 1934

Superfamily **PLECTAMBONITACEA** Jones, 1928

Family **PLECTAMBONITIDAE** Jones, 1928

Subfamily **AHTIELLINAE** Öpik, 1933

Genus ***BORUA*** nov.

DIAGNOSIS. Medium-sized, moderately to strongly transversely semi-elliptical to semicircular plectambonitids, with strongly resupinate lateral and anterior margins, external surfaces smooth or with faint peripheral parvicostellate ornamentation crossed by faint impersistent concentric rugae; ventral interarea planar, strongly apsacline to orthocline, delthyrium closed posteriorly by gently arched pseudodeltidium, dorsal interarea narrow, planar, anacline, notothyrium covered by gently arched chilidium.

Ventral interior with small, triangular teeth supported by short, receding, subparallel dental plates, flanking semi-elliptical muscle platform defined by fine, elevated, rounded rim; floor of valve with two narrow, subparallel canals of *vascula myaria* possibly representing saccate ventral mantle canal system, elevated subperipheral rim well-developed on floor of valve at point of resupination.

Dorsal interior with short, thickened brachiophores flanked by small, deeply incised sockets defined by elevated fulcral plates, notothyrium narrowly triangular, surmounted by low, ridge-like cardinal process; floor of valve with prominent subparallel rim developed at point of resupination; dorsal mantle canal system unknown.

NAME. After Brian Boru (926–1014), ancient High King of Ireland.

TYPE SPECIES. *Borua modesta* sp. nov., from the Tourmakeady Limestone, Co. Mayo.

DISCUSSION. The Irish specimens possess all the characteristics of the Ahtiellinae, but can readily be distinguished from all previously described genera in the subfamily. *Ahtiella* Öpik differs in possessing a well-developed radial ornamentation, a dorsal sulcus, and, internally, a prominent median septum in the brachial valve. *Inversella* Öpik, and *Ukoa* Öpik, on the other hand, are immediately distinguished by their external ornamentation – the former having strongly developed rugae and the latter having a distinctive parvicostellate ornamentation and pedicle foramen. Both *Gutasella* Neuman and *Reinversella* Bates differ from the Irish specimens in being doubly geniculate peripherally. In addition *Gutasella* lacks elevated subperipheral platforms internally. *Schedophyla* Neuman is also distinguished by its strong parvicostellate ornamentation, and a convex brachial valve. Only the brachial valve of *Rutrumella* Harper is known, but close affinity with the new Irish genus is ruled out by the presence, in the former, of a prominent dorsal median septum.

The new genus is at present monospecific, and known only from the Tourmakeady Limestone.

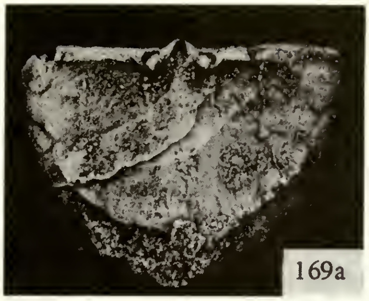
Borua modesta sp. nov.

Figs 169–175

DIAGNOSIS. Medium-sized, plano-convex, moderately to strongly semi-elliptical to semicircular *Borua*; pedicle valve gently convex, on average 77% as long as wide and 25% as deep as long; brachial valve planar with strong peripheral resupination, on average 70% as long as wide and 22% as deep as long; ventral muscle platform semi-elliptical, on average 79% as long as wide.

NAME. 'Moderate'.

DESCRIPTION. Medium-sized, moderately to strongly transversely semi-elliptical to semicircular *Borua*, plano-convex in profile with strongly resupinate lateral and anterior margins;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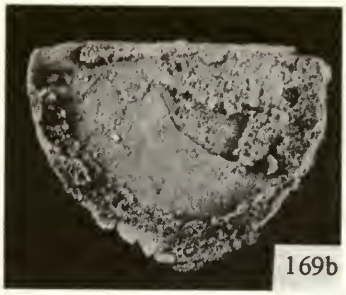
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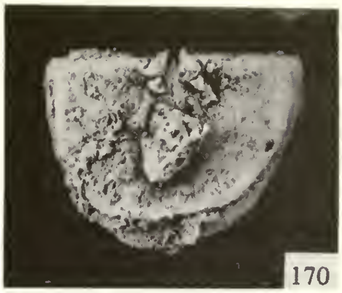
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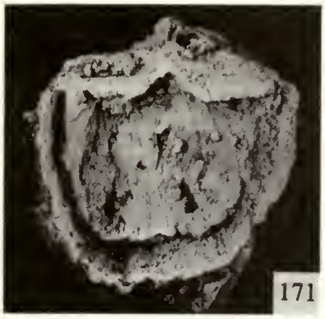
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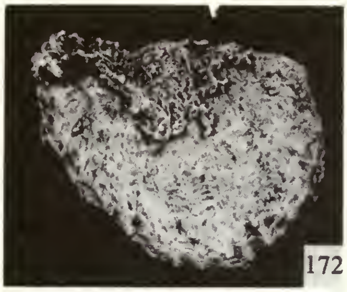
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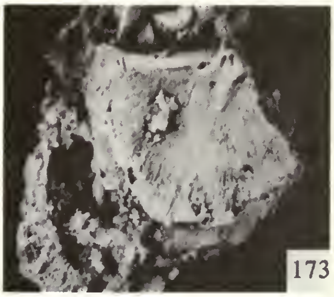
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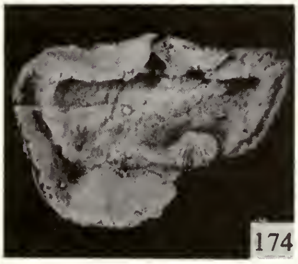
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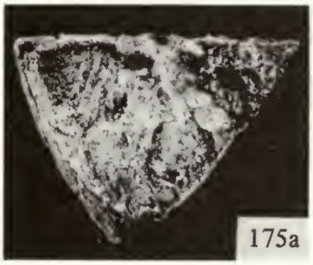
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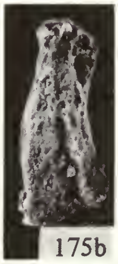
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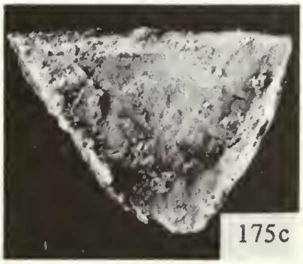

175c

Figs 169–175 *Borua modesta* gen. et sp. nov. Fig. 169a, b, **holotype** BB 95531, interior and exterior of brachial valve, both ×3; Fig. 170, paratype BB 95535, interior of brachial valve, ×3; Fig. 171, paratype BB 95532, interior of pedicle valve, ×3; Fig. 172, paratype BB 95534, exterior of pedicle valve, ×3; Fig. 173, paratype BB 95533, interior of incomplete brachial valve, ×3; Fig. 174, paratype BB 95536, interior of incomplete pedicle valve, ×3; Fig. 175a, b, c, paratype BB 95537, internal, lateral and exterior views of incomplete brachial valve, all ×4.

pedicle valve gently convex, ranging from strongly transversely semi-elliptical to slightly elongately semicircular, on average 77% as long as wide (ranging from 51% as long as wide to 97% as wide as long in 4 specimens) and 25% as deep as long (range 21–31%; n = 3); brachial valve planar, with strong peripheral resupination, on average 70% as long as wide ($\bar{l}$ mm (var l) 8·33 (0·709), $\bar{w}$ mm (var w) 11·89 (0·148), r = 0·526; n = 7) and with a maximum thickness at resupinate anteromedian margin averaging 22% of valve length ($\bar{l}$ mm (var l) 8·33 (0·709), $\overline{th}$ mm (var th) 1·84 (0·053), r = 0·458; n = 7); external ornamentation smooth or with faint unequally parvicostellate ornamentation developed peripherally on trail, crossed by rare, impersistent, concentric rugae; ventral interarea planar, strongly apsacline to orthocline, extending anteriorly on average for 18% of valve length (range 14–20%; n = 3), triangular delthyrium closed posteriorly by gently arched pseudodeltidium; dorsal interarea narrow, planar, anacline notothyrium covered by gently arched chilidium.

Ventral interior with small, thickened teeth supported by short, receding, thickened, subparallel, dental plates, flanking poorly-defined transversely semi-elliptical ventral muscle platform on average 79% as long as wide (range 75–82%; n = 3); ventral mantle canal system possibly saccate, with two subparallel canals of *vascula myaria* measuring 0·3 mm wide in one specimen.

Dorsal interior with short, thickened, tapering brachiophores extending anteriorly for an average of 13% of valve length ($\bar{l}$ mm (var l) 8·33 (0·709), $\bar{l}_b$ (var l_b) 1·10 (0·007), r = 0·685; n = 7) flanked by small, deeply-incised, sockets extending laterally for an average of 25% of valve width ($\bar{w}$ mm (var w) 11·89 (0·148), $\bar{w}_{so}$ mm (var w_{so}) 2·94 (0·050), r = 0·844; n = 7); notothyrial platform narrowly triangular on average 99% as long as wide ($\bar{l}_n$ mm (var l_n) 0·87 (0·280), $\bar{w}_n$ mm (var w_n) 0·87 (0·022), r = 0·954; n = 9) with narrow, ridge-like, rounded, median cardinal process; notothyrial platform buttressed medially by variably-developed, very short, median ridge.

HOLOTYPE. Brachial valve; BB 95531: length 9·1 mm, width 12·1 mm. Fig. 169.

		length	width (mm)
PARATYPES.	Pedicle valve; BB 95532	9·9	10·2
	Pedicle valve; BB 95534	9·4	11·4
	Pedicle valve; BB 95536	7·8	12·3
	Brachial valve; BB 95535	8·8	11·6
	Incomplete brachial valve; BB 95533	8·2	–
	Incomplete brachial valve; BB 95537	7·2	–

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. Statistical analysis of the main shape parameters of this species demonstrates its high degree of morphological variability, particularly in shell outline. However, ornamentation and internal morphology are standard throughout, confirming the taxonomic homogeneity of the sample.

Family **LEPTELLINIDAE** Ulrich & Cooper, 1936

Subfamily **LEPTELLININAE** Ulrich & Cooper, 1936

Genus ***TOURMAKEADIA*** nov.

DIAGNOSIS. Medium-sized, transversely semi-elliptical, concavo-convex leptellinids; pedicle valve moderately convex, brachial valve shallowly to moderately concave; external ornamentation costellate to parvicostellate; ventral interarea gently concave, apsacline, with broad, triangular, open delthyrium, dorsal interarea narrow, anacline, notothyrium open.

Ventral interior with small triangular teeth supported by short, strongly receding, divergent, dental plates flanking undifferentiated, sessile, transversely semicircular ventral muscle platform; floor of pedicle valve with prominent, radially striated, anteriorly bilobed, subperipheral platform defined peripherally by elevated striated ridge, ventral mantle canal system unknown.

Dorsal interior with slender, tapering, anteriorly diverging brachiophores flanked by shallow sockets; brachiophores supported laterally by inclined brachiophore bases sloping gently inwards to define broadly triangular, anteriorly bilobed, slightly concave, notothyrial platform surmounted medially by low, gently rounded, ridge-like, cardinal process; floor of valve with prominent, radially striated, anteriorly bilobed, subperipheral platform defined peripherally by elevated striated ridge; dorsal mantle canal system unknown.

NAME. From the locality of Tourmakeady.

TYPE SPECIES. *Tourmakeadia fimbriata* sp. nov., from the Tourmakeady Limestone, Co. Mayo.

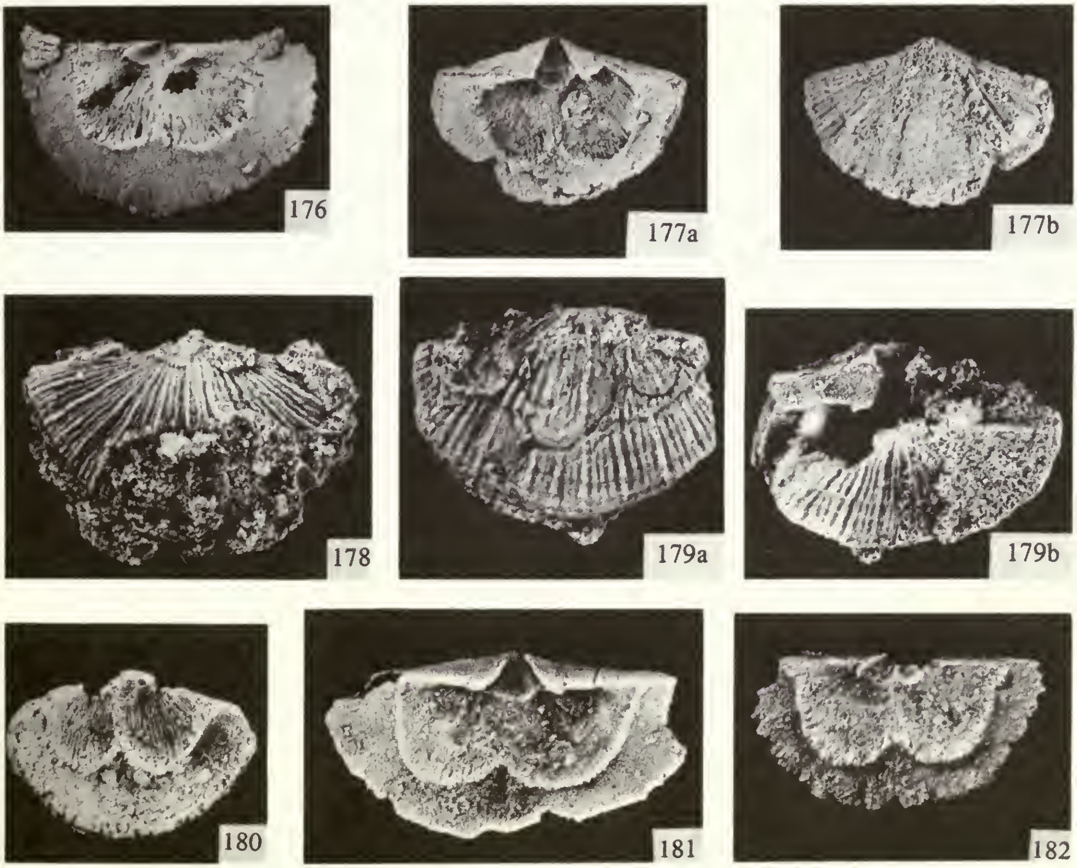
DISCUSSION. The concavo-convex profile, prominent subperipheral platforms in both valves, and characteristic dorsal cardinalia confirm that the taxonomic affinities of the new stock lies with the Leptellinae. Within the subfamily, *Tourmakeadia* most closely resembles *Anaptambonites* Williams in external form, although the latter genus has a much finer ornamentation. Internally, however, the differences between the two stocks are much more apparent in that *Anaptambonites* lacks a subperipheral platform in the ventral valve, and has a prominent dorsal median septum and a massive, differentiated, cardinal process. Although *Calytolepta* Neuman has internal subperipheral platforms in both valves, it is readily distinguished from the new genus by having a pronounced parvicostellate external ornamentation, a chilidium, an apically perforate pseudodeltidium, and internally a dorsal median septum.

Tourmakeadia is at present known only from the new species found in the Tourmakeady Limestone.

Tourmakeadia fimbriata sp. nov.

Figs 176–182

Diagnosis. Medium-sized, transversely semi-elliptical, concavo-convex *Tourmakeadia*; ped-



Figs 176–182 *Tourmakeadia fimbriata* gen. et sp. nov. Fig. 176, **holotype** BB 95538, interior of brachial valve, ×5; Fig. 177a, b, paratype BB 95539, interior and exterior of incomplete pedicle valve, both ×4; Fig. 178, paratype BB 95543, ventral view of conjoined valves, ×4; Fig. 179a, b, paratype BB95541, ventral and oblique posterior views of conjoined valves, both ×5; Fig. 180, paratype BB 95544, interior of incomplete pedicle valve, ×5; Fig. 181, paratype BB 95542, interior of incomplete pedicle valve, ×4; Fig. 182, paratype BB 95540, interior of incomplete brachial valve, ×6.

icle valve moderately convex averaging 59% as long as wide and 37% as deep as long; brachial valve shallowly to moderately concave, averaging 49% as long as wide and 25% as deep as long; external ornamentation costellate or slightly parvicostellate, with 4 to 5 rounded ribs per mm at 2 mm anteromedially of dorsal umbo.

NAME. 'Hemmed'.

DESCRIPTION. Medium-sized, transversely semi-elliptical, concavo-convex *Tourmakeadia*; pedicle valve moderately convex averaging 59% as long as wide (range 55–62%; n = 4) and 37% as deep as long (range 36–38%; n = 3); brachial valve shallowly to moderately concave, averaging 49% as long as wide ($\bar{l}$ mm (var l) 4·40 (0·282), $\bar{w}$ mm (var w) 8·94 (1·199), r = 0·957; n = 12) and 25% as deep as long ($\bar{l}$ mm (var l) 4·24 (0·300), $\overline{th}$ mm (var th) 1·06 (0·020), r = 0·762; n = 8); lateral and anterior margins of both valves smoothly rounded; external ornamentation costellate to slightly parvicostellate with 4 or 5 rounded ribs per mm at 2 mm anteromedially of umbones of 5 and 4 brachial valves respectively; triangular ventral interarea gently concave, apsacline, with broad, triangular, open delthyrium, dorsal interarea narrow, anacline, notothyrium open.

Ventral interior with small triangular teeth supported by short, strongly receding, divergent dental plates flanking undifferentiated, moderately to strongly transversely semicircular, sessile, ventral muscle platform with elevated anterior and anterolateral margins averaging 78% as long as wide (range 68–88%; n = 2); floor of pedicle valve with prominent, radially striated, subperipheral platform defined by elevated, striated, ridge strongly bilobed anteromedially and averaging 53% as long as wide (range 46–60%; n = 2).

Dorsal interior with slender, tapering, anteriorly divergent brachiophores, extending anteriorly on average for 20% of valve length ($\bar{l}$ mm (var l) 4·44 (0·396), $\bar{l}_b$ mm (var l_b) 0·89 (0·008), r = 0·660; n = 7), brachiophores flanked by shallow sockets extending laterally on average for 28% of valve width ($\bar{w}$ mm (var w) 8·93 (1·694), $\bar{w}_{so}$ mm (var w_{so}) 2·50 (0·083), r = 0·763; n = 8) and supported by gently inclined brachiophore bases defining broadly triangular, anteriorly bilobed, notothyrial platform extending anteriorly for an average for 19% of valve length ($\bar{l}$ mm (var l) 4·35 (0·403), $\bar{l}_n$ mm (var l_n) 0·87 (0·007), r = 0·926; n = 6), and averaging 64% as long as wide ($\bar{l}_n$ mm (var l_n) 0·87 (0·007), $\bar{w}_n$ (var w_n) 1·37 (0·019), r = 0·956; n = 6); floor of valve with prominent, radially striated, subperipheral platform, strongly bilobed anteromedially, defined by elevated striated ridge extending anteriorly for an average of 56% of valve length (range 52–60%; n = 5) and averaging 45% as long as wide (range 43–48%; n = 5).

HOLOTYPE. Brachial valve; BB 95538: length 4·5 mm, width 7·5 mm. Fig. 176.

		length	width (mm)
PARATYPES.	Conjoined valves; BB 95543a, b	6·1	11·0
	Incomplete conjoined valves; BB 95541a, b	5·5	–
	Incomplete conjoined valves; BB 95545a, b	–	–
	Incomplete pedicle valve; BB 95539	–	–
	Incomplete pedicle valve; BB 95542	–	–
	Incomplete pedicle valve; BB 95544	–	–
	Brachial valve; BB 95540	3·6	7·2

TYPE HORIZON AND LOCALITY. Loc. 1.

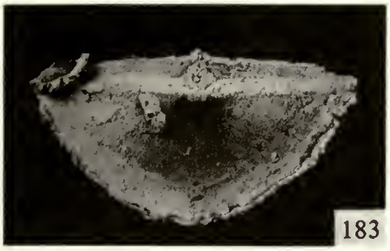
Subfamily **LEPTELLINAE** Williams, 1965

Genus ***LEPTELLA*** Hall & Clarke, 1892

Leptella musculosa sp. nov.

Figs 183–189

DIAGNOSIS. Medium-sized, moderately to strongly semi-elliptical or subquadrate *Leptella*,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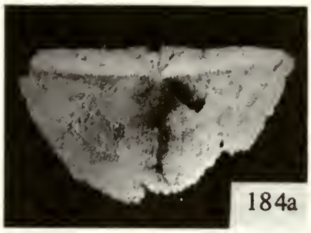
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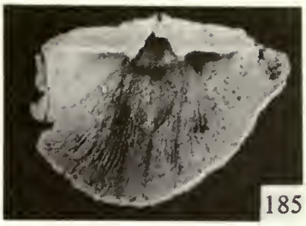
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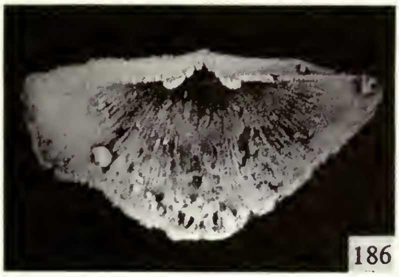
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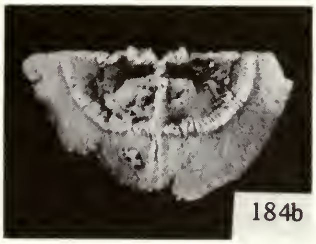
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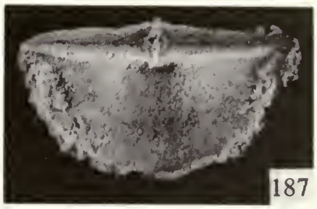
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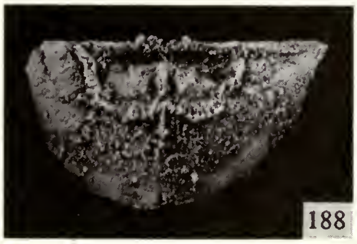
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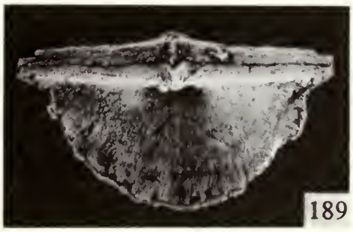
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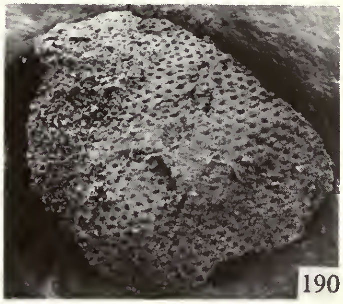
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Figs 183–189 *Leptella musculosa* sp. nov. Fig. 183, **holotype** BB 95546, dorsal view of conjoined valves, ×5; Fig. 184a, b, paratype BB 95549, exterior and interior of brachial valve, both ×5; Fig. 185, paratype BB 95550, interior of incomplete pedicle valve, ×4; Fig. 186, paratype BB 95548, interior of pedicle valve, ×5; Fig. 187, paratype BB 95552, dorsal view of conjoined valves, ×5; Fig. 188, paratype BB 95547, interior of brachial valve, ×5; Fig. 189, paratype BB 95600, dorsal view of conjoined valves, ×6.

Fig. 190 *Punctolira*? sp. BB 95601, fragment, ×15.

pedicle valve moderately convex, averaging 63% as long as wide and 36% as deep as long, brachial valve moderately concave averaging 58% as long as wide and 41% as deep as long.

NAME. 'Muscled'.

DESCRIPTION. Medium-sized, moderately to strongly semi-elliptical or subquadrate *Leptella*, pedicle valve moderately convex, averaging 63% as long as wide ($\bar{l}$ mm (var l) 4·36 (1·394), $\bar{w}$ mm (var w) 6·93 (2·305), r = 0·897; n = 59) and 36% as deep as long ($\bar{l}$ mm (var l) 4·36 (1·394), $\overline{th}$ mm (var th) 1·58 (0·376), r = 0·920; n = 59), brachial valve moderately concave averaging 58% as long as wide ($\bar{l}$ mm (var l) 4·28 (1·027), $\bar{w}$ mm (var w) 7·38 (2·382), r = 0·887; n = 52) and 41% as deep as long ($\bar{l}$ mm (var l) 4·28 (1·027), $\overline{th}$ mm (var th) 1·76 (1·028), r = 0·859; n = 47); lateral and anterior margins of both valves smoothly rounded, anterior margin with broad, gently curved sulcus in pedicle valve; external shell surfaces smooth, rarely with fine, faint, unequal parvicostellae; ventral interarea broad, triangular, curved, orthocline, delthyrium sealed by moderately arched triangular pseudodeltidium, dorsal interarea broad, triangular, planar, strongly hypercline.

Ventral interior with short, thickened, triangular teeth supported by short, poorly-developed, subparallel, receding dental plates forming lateral margins of moderately well-defined, broadly triangular, ventral muscle field averaging 88% as long as wide ($\bar{l}_{sc}$ mm (var l_{sc}) 1·22 (0·014), $\bar{w}_{sc}$ (var w_{sc}) 1·38 (0·006), r = 0·720; n = 18) defined by low, rounded, elevated ridge of shell anteriorly and composed of large, median, triangular adductor scar extending anteriorly of small, narrowly triangular, flanking diductor scars, floor of valve occasionally with faint radial striae numbering up to 10 per mm at 5 mm anteromedially of umbo.

Dorsal interior with flattened, spatulate, erect brachiophores flanked by narrow, triangular sockets extending laterally on average for 22% of valve width ($\bar{w}$ mm (var w) 7·59 (1·987), $\bar{w}_{so}$ mm (var w_{so}) 1·68 (0·947), r = 0·834; n = 34), brachiophores supported by thickened, rounded, brachiophore bases continuous with well-developed chilidial plates defining small, triangular, shallowly concave, notothyrial platform averaging 69% as wide as long ($\bar{l}_n$ mm (var l_n) 0·63 (0·008), $\bar{w}_n$ mm (var w_n) 0·43 (0·007), r = 0·872; n = 29) covered posteriorly by gently arched, narrowly triangular chilidium; floor of brachial valve with well-developed, broadly semi-elliptical lophophore platform strongly elevated peripherally and averaging 42% as long as wide ($\bar{l}_{lp}$ mm (var l_{lp}) 2·08 (1·321), $\bar{w}_{lp}$ mm (var w_{lp}) 4·93 (2·143), r = 0·893; n = 39), lophophore platform bilobed anteriorly at narrow, low, subtriangular median septum arising on floor of valve anteriorly of notothyrial platform and extending almost to anterior margin of valve; floor of valve with pair of elongately crescentic adductor muscle scars impressed symmetrically on either side of median septum posteriorly of elevated rim of lophophore platform and averaging 53% as wide as long ($\bar{l}_{sc}$ mm (var l_{sc}) 1·28 (0·183), $\bar{w}_{sc}$ mm (var w_{sc}) 0·68 (0·037), r = 0·898; n = 15), floor of valve occasionally with fine radial striae numbering up to 10 per mm at 5 mm anteromedially of umbo.

HOLOTYPE. Conjoined valves; BB 95546a, b: length 4·9 mm, width 9·1 mm. Fig. 183.

		length	width (mm)
PARATYPES.	Conjoined valves; BB 95552a, b	3·9	6·8
	Conjoined valves; BB 95600a, b	4·4	7·9
	Pedicle valve; BB 95548	5·2	9·3
	Incomplete pedicle valve; BB 95550	–	–
	Brachial valve; BB 95549	4·6	7·9
	Incomplete brachial valve; BB 95547	–	7·8
	Incomplete brachial valve; BB 95551	–	–

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. The lack of a cardinal process internally and of a consistent radial ornamentation externally, combined with a strongly concavo-convex profile and characteristic dorsal cardinalia and lophophore platform, confirm that the Tourmakeady specimens are representatives of *Leptella*. Internally the Irish specimens are similar to the closely-related leptellin genus *Petroria* Wilson, although the latter genus lacks dental plates. Externally the two genera are readily distinguishable as *Petroria* has a prominent wavy, lamellose ornamentation (Cooper 1956: 747).

In size and shape the Irish specimens are similar to *Leptella sordida* (Billings), the type species of the genus, from the Lower Ordovician Levis Shales of Quebec (Ulrich & Cooper 1938: 189). However, the status of the Irish material as a new species is confirmed by the fact that *L. sordida* has a broader median septum, and much stronger and thicker brachiophores. In addition the well-developed dorsal adductor scars of *L. musculosa* are not evident in illustrations of *L. sordida*, nor are they mentioned in the accompanying description (Ulrich & Cooper 1938: 189). A further distinguishing feature is the unequally parvicostellate ornamentation of *L. sordida*, which, although faint, is better developed than on any Irish specimen.

Suborder **SYNTROPHIDINA** Ulrich & Cooper, 1936

Superfamily **PORAMBONITACEA** Davidson, 1853

Family **TETRALOBULIDAE** Ulrich & Cooper, 1936

Genus ***PUNCTOLIRA*** Ulrich & Cooper, 1936

Punctolira? sp.

Fig. 190

The Tourmakeady residues yielded a single incomplete specimen (BB 95601) with a distinctive, pitted, external ornamentation, similar to that which characterizes *Punctolira*, a small tetralobulid genus from Lower Ordovician successions in North America. Internally the only morphological details discernible in the Tourmakeady fragment are the incomplete remnants of a pair of well-developed lateral septa. With such inadequate criteria, generic identification cannot be made with certainty.

Family **CLARKELLIDAE** Schuchert & Cooper, 1931

Genus *ACANTHOGLYPHA* nov.

Diagnosis. Medium-sized, transversely subquadrate clarkellid, pedicle valve moderately to strongly convex, brachial valve moderately convex with variably-developed anterior plication; external shell surface with closely spaced concentric ornamentation bearing dense concentric and radial arrays of hollow, erect to prone, spines each branching dichotomously anteriorly; ventral interarea triangular, strongly curved, anacline, delthyrium open, dorsal interarea narrow, slightly curved, anacline with open delthyrium.

Ventral interior with small, flattened, teeth supported by receding, convergent, dental plates forming lateral margins of elevated, tongue-shaped, spondylium supported by strong, thickened, median ridge; floor of valve with two pairs of narrow canals of digitate mantle canal system.

Dorsal interior with short, curved, thickened, triangular brachiophores supported by short, divergent bases sloping sharply down to valve floor to form lateral margins of broadly triangular, sessile, notothyrial platform; floor of valve with two discrete pairs of strongly elevated, elongately oval, adductor muscle scars; and three pairs of narrow, radiating branches of digitate mantle canal system.

Name. Greek, *ἀκανθώδης*, thorny + *γλῠφή*, carving.

Type species. *Acanthoglypha affinis* (Reed), from the Tourmakeady Limestone and associated sediments, Co. Mayo.

Discussion. The distinctive association of a spondylium in the pedicle valve with small divergent brachiophore bases in the brachial valve confirms that the new genus is a representative of the Clarkellidae. Indeed the internal morphology of the pedicle valve of *Acanthoglypha* is virtually identical to that of other clarkellid genera such as *Thaumotrophia* Wang or *Stichotrophia* Cooper. However, the presence of dorsal muscle bases and, in particular, the nature of the external ornamentation, immediately distinguish *Acanthoglypha* from other clarkellid genera. The new Irish genus is closest to *Calliglypha* Cloud; internally the two stocks are similar, although the latter lacks prominent elevated dorsal muscle bases. Apart from this feature the chief differentiation between the two genera is the nature of the external ornamentation – dense spines in *Acanthoglypha* as compared with the radial and concentric nodes characteristic of *Calliglypha* (Cloud 1948). Dr G. A. Cooper kindly examined the type specimens of *Calliglypha* in the United States National Museum, Washington D.C., on our behalf and has confirmed that there is no suggestion of spines (Cooper, personal communication 1982). In addition, every specimen of *Acanthoglypha* from the Tourmakeady Limestone was closely examined to determine the proportion on which, as a result of silicification or poor preservation, spines were not discernible. Out of a total sample of 164 specimens or fragments, no fewer than 142 (= 86·6%) had clear evidence of external spines. It is thus unlikely that the absence of spines on *Calliglypha* is a result of imperfect preservation, and hence the distinction between the two genera is substantiated.

Acanthoglypha affinis (Reed)

Figs 191–198

1909 *Streptis affinis* Reed *in* Gardiner & Reynolds: 151; pl. 6, figs 14a, b.
1978 *Calliglypha affinis* (Reed) Cocks: 136.

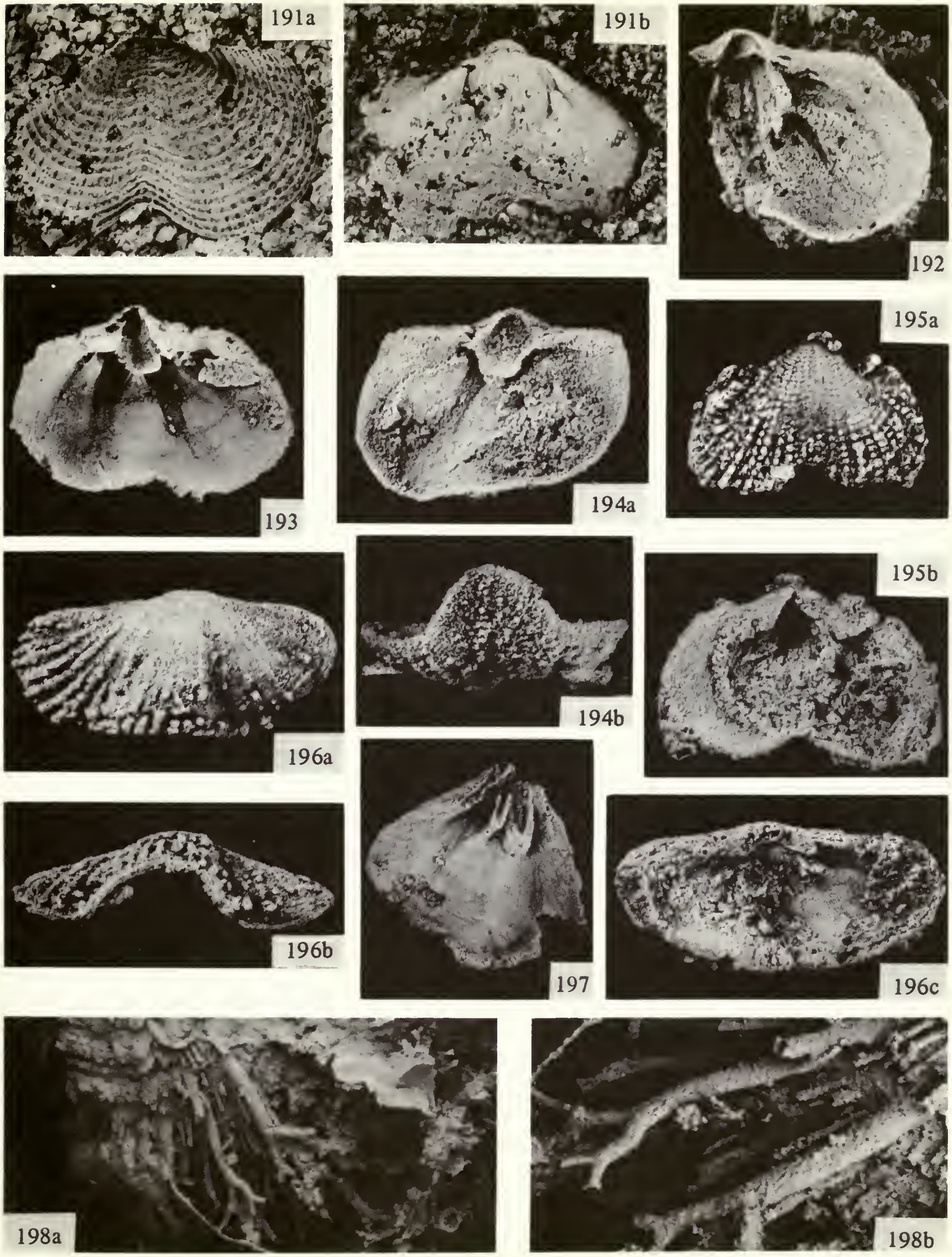
Diagnosis. Medium-sized, subquadrate *Acanthoglypha*; pedicle valve moderately to strongly convex, averaging 64% as long as wide and 60% as deep as long; brachial valve moderately convex, averaging 47% as long as wide and 47% as deep as long; external surfaces with dense radial and concentric arrays of fine and coarse bifurcating hollow spines with maximum diameters of 50 μm and 200 μm, respectively.

Description. Medium-sized, transversely subquadrate *Acanthoglypha*; pedicle valve moderately to strongly convex, averaging 64% as long as wide ($\bar{l}$ mm (var l) 6·24 (1·216), $\bar{w}$ mm (var w) 9·79 (2·211), r = 0·952; n = 7) and 60% as deep as long ($\bar{l}$ mm (var l) 6·12 (1·326), $\overline{th}$ mm (var th) 3·70 (0·544), r = 0·982; n = 6); brachial valve moderately convex averaging 47% as long as wide ($\bar{l}$ mm (var l) 5·35 (1·086), $\bar{w}$ mm (var w) 11·46 (6·706), r = 0·990; n = 8), and 47% as deep as long ($\bar{l}$ mm (var l) 5·35 (1·086), $\overline{th}$ mm (var th) 2·51 (0·327), r = 0·975; n = 8); lateral margins of both valves strongly rounded, anterior margins gently rounded, with variably-developed, narrow, rectangular uniplication with an average maximum width of 2·8 mm in 3 adult specimens (range 2·6–3·0 mm); external shell surfaces with strong, closely and regularly spaced concentric ornamentation bearing dense radial and concentric arrays of hollow, erect to prone, fine and coarse spines branching dichotomously anteriorly, with maximum lengths and diameters of 0·6 mm and 50 μm and 2·0 mm and 200 μm, respectively, fine spines inserted when separation between larger spines exceeds 0·4 mm; ventral interarea triangular, strongly curved, anacline, delthyrium open, dorsal interarea narrow, slightly curved, anacline, with open notothyrium.

Ventral interior with small, flattened teeth supported by receding, convergent, dental plates forming lateral margins of elevated, tongue-shaped spondylium averaging 62% as wide as long ($\bar{l}_{sp}$ mm (var l_{sp}) 2·13 (0·025), $\bar{w}_{sp}$ mm (var w_{sp}) 1·31 (0·018), r = 0·930; n = 7), spondylium supported by strong, thickened, median ridge and flanked laterally by low, flattened, bosses of shell separating two pairs of narrow canals, up to 0·4 mm wide, of digitate mantle canal system.

Dorsal interior with short, curved, thickened, triangular brachiophores flanked by elongate, narrow, shallow sockets, brachiophores supported by short, divergent brachiophore bases sloping sharply down to valve floor to form lateral margins of broadly triangular, sessile, notothyrial platform averaging 65% as long as wide (range 59–67%; n = 5); floor of valve with two discrete pairs of elevated adductor muscle scars, with a narrow elongate, anteriorly divergent, pair averaging 36% as wide as long ($\bar{l}_{sc}$ mm (var l_{sc}) 1·18 (0·064), $\bar{w}_{sc}$ mm (var w_{sc}) 0·42 (0·004), r = 0·845; n = 9) situated posterolaterally, and a broad, spatulate, subparallel pair symmetrically disposed on either side of short, low, median ridge and averaging 62% as wide as long ($\bar{l}_{sc}$ mm (var l_{sc}) 1·31 (0·066), $\bar{w}_{sc}$ mm (var w_{sc}) 0·81 (0·014), r = 0·787; n = 9), three pairs of narrow canals, 0·7 mm wide posteriorly tapering to 0·2 mm anteriorly, of digitate mantle canal system radiating anteriorly from between, and laterally of, muscle scars.

Lectotype. Natural external and internal moulds of incomplete brachial valve. Sedgwick Museum, Cambridge, reg. no. A10379a, b (Fig. 191a, b). Sel. Cocks 1978: 136; fig'd Reed *in* Gardiner & Reynolds 1909: pl. 6, figs 14a, b. From coarse ash near Shangort, Tourmakeady, Co. Mayo. Fig. 191.



Figs 191–198 *Acanthoglypha affinis* (Reed). Fig. 191a, b, lectotype (sel. Cocks 1978: 136) SM A10379a, b, external natural mould of incomplete brachial valve (a) and its corresponding internal mould (b), both ×5; from coarse ash near Shangort, Tourmakeady. Fig. 192, BB 95579, interior of incomplete brachial valve, ×4; Fig. 193, BB 95577, interior of pedicle valve, ×5; Fig. 194a, b, BB 95575, interior and anterior views of pedicle valve, both ×5; Fig. 195a, b, BB 95576, exterior and anterior of brachial valve: a, ×4; b, ×5; Fig. 196a, b, c, BB 95574, exterior, anterior and interior views of brachial valve, all ×4; Fig. 197, BB 95578, interior of incomplete brachial valve, ×4; Fig. 198a, b, BB 95580, branching spines on fragment: a, ×14; b, ×32.

		length	width (mm)
Figured material.	Pedicle valve; BB 95575	5·5	8·0
	Pedicle valve; BB 95577	5·3	8·4
	Brachial valve; BB 95574	5·2	11·6
	Brachial valve; BB 95576	4·8	8·6
	Incomplete brachial valve; BB 95578	–	–
	Incomplete brachial valve; BB 95579	7·1	–
	Fragment; BB 95580	–	–

All Loc. 1.

Discussion. In 1909 Reed described a new species, *Streptis affinis*, in an appendix to the account of the geology of the Tourmakeady district by Gardiner & Reynolds. The species was founded on the natural external and internal moulds of an almost complete brachial valve (not a pedicle valve as stated by Reed), and several small fragments of shell, collected from a coarse ash. These moulds, constituting the lectotype of the species, the genotype of *Acanthoglypha*, were subsequently presented to the Sedgewick Museum, Cambridge, by Gardiner. They are illustrated herein (Fig. 191a, b) along with representative etched specimens of *Acanthoglypha affinis* from the Tourmakeady Limestone, with which they are conspecific. Reed's assignment of his specimens to the triplesiacean genus *Streptis* is somewhat surprising, even allowing for his misinterpretation of the lectotype as a pedicle valve, because the shell possesses none of the characters diagnostic of this superfamily.

A. affinis (Reed) is at present the sole known representative of the new genus.

Genus ***SYNTROPHINA*** Ulrich *in* Weller & St Clair, 1928

Syntrophina magna sp. nov.

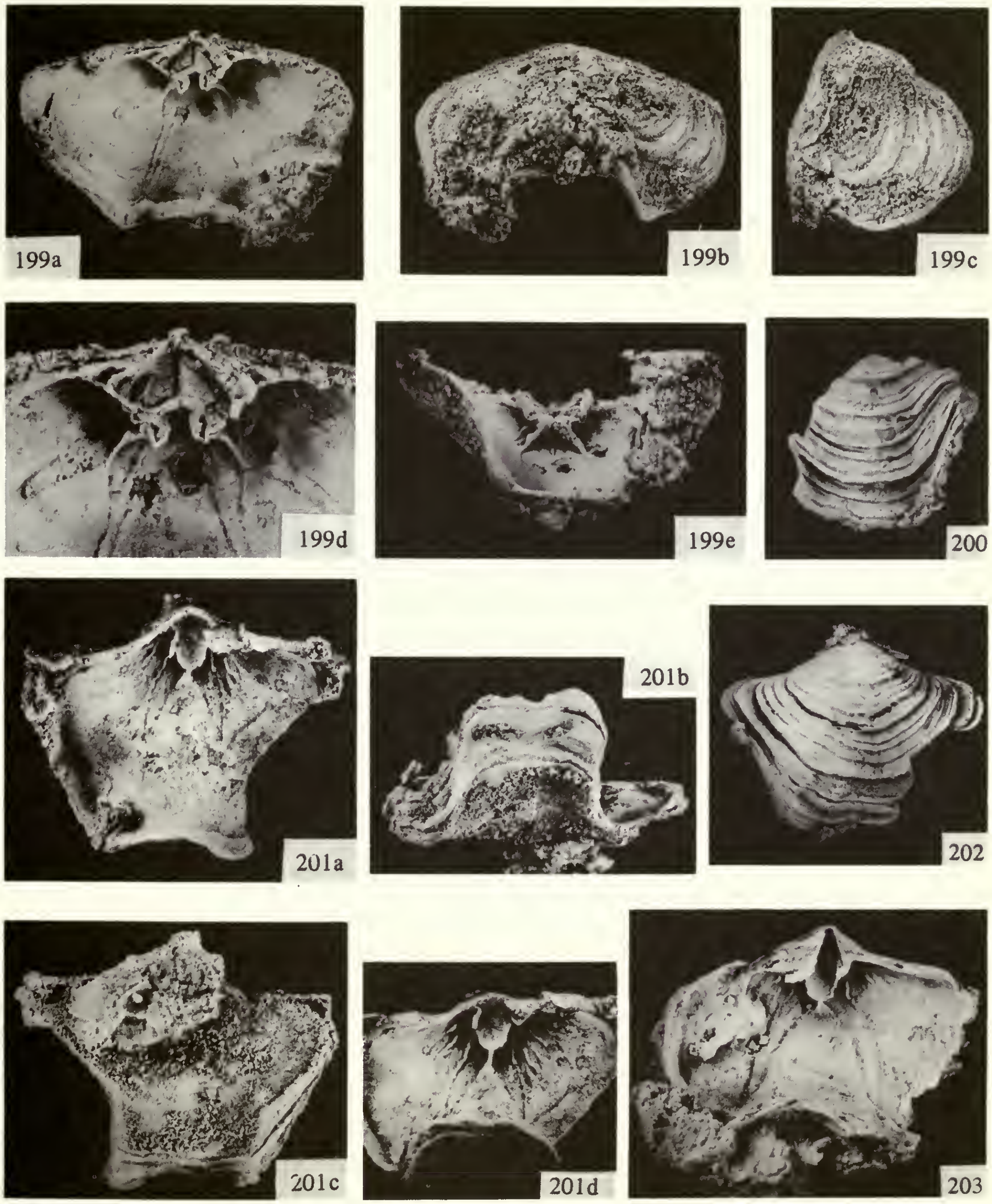
Figs 199–203

Diagnosis. Large, broadly semi-elliptical *Syntrophina*; pedicle valve moderately convex averaging 76% as long as wide and 43% as deep as long; brachial valve moderately to strongly convex averaging 71% as long as wide and 56% as deep as long; external shell surfaces ornamented by regularly-spaced concentric lamellae with an average spacing of 0·7 mm.

Name. 'Large'.

Description. Large, broadly semi-elliptical, strong uniplicate *Syntrophina*; pedicle valve moderately convex, averaging 76% as long as wide ($\bar{l}$ mm (var l) 12·40 (4·33), $\bar{w}$ mm (var w) 16·30 (8·43), r = 0·989; n = 7) and 43% as deep as long ($\bar{l}$ mm (var l) 12·32 (4·38), $\overline{th}$ mm (var th) 5·33 (1·29), r = 0·942; n = 6); brachial valve moderately to strongly convex, averaging 71% as long as wide (range 62–76%; n = 3) and 56% as deep as long (range 50–64%; n = 3); lateral margins of both valves gently rounded, becoming moderately geniculate in adult growth stages, anterior margins of both valves gently rounded or truncated, with strong rectangular, geniculate, ventral sulcus attaining a maximum width averaging 48% (range 44–53%; n = 4) of valve width; external shell surfaces ornamented by closely spaced concentric lamellae with an average spacing of 0·72 mm (range 0·4–1·0 mm; n = 16) and 0·71 mm (range 0·5–1·0 mm; n = 12) in two adult valves; ventral interarea narrow, curved, apsacline, dorsal interarea very narrow, gently curved, anacline.

Ventral interior with short, thickened teeth supported by well-developed convergent dental plates contiguous with margins of prominent, elongate, spatulate spondylium averaging 46% as wide as long (range 41–50%; n = 3), sessile posteriorly but strongly elevated anteriorly and anterolaterally and supported medially by short, narrow, ridge not extending anteriorly beyond margin of spondylium, median ridge flanked by at least two pairs of short, low ridges radiating posterlaterally from beneath spondylium; floor of valve with well-developed digitate mantle canal system with short trunks of *vascula genitalia*



Figs 199–203 *Syntrophina magna* sp. nov. Fig. 199a, b, c, d, e, **holotype** BB 95553, brachial valve: a, interior, ×3; b, exterior, ×3; c, lateral view, ×3; d, dorsal cardinalia, ×5; e, anterior view, ×3; Fig. 200, paratype BB 95559, exterior of incomplete pedicle valve, ×3; Fig. 201a, b, c, d, paratype BB 95554, incomplete pedicle valve: a, interior view, ×2; b, anterior view, ×2; c, exterior view, ×2; d, oblique external view, ×2; Fig. 202, paratype BB 95557, exterior of pedicle valve, ×2; Fig. 203, paratype BB 95555, interior of pedicle valve, ×3.

impressed posterolaterally and pair of long, narrow, subparallel canals, up to 0·5 mm wide, of *vascula media* extending almost to anterior margin of valve.

Dorsal interior with short, thickened, flattened brachiophores flanked by broad sockets defined by gently concave fulcral plates; brachiophores supported dorsally by gently curved brachiophore bases extending anteriorly beneath brachiophores as rounded lobes curving in towards median axis of valve; brachiophore bases contiguous with triangular notothyrial platform with dimensions of 2·1 × 2·0 mm and 1·7 × 1·5 mm in two specimens, strongly elevated above valve floor and supported by pair of short, divergent, narrow ridges; floor of valve with two pairs of narrow trunks of equidistributed digitate mantle canal system, up to 0·5 mm wide, radiating anterolaterally from beneath dorsal cardinalia.

HOLOTYPE. Brachial valve; BB 95553: length 11·8 mm, width 18·3 mm. Fig. 199.

		length	width (mm)
PARATYPES.	Pedicle valve; BB 95554	14·7	19·0
	Pedicle valve; BB 95555	12·6	17·3
	Pedicle valve; BB 95557	12·8	17·2
	Incomplete pedicle valve; BB 95559	–	–
	Incomplete brachial valve; BB 95556	8·4	–
	Incomplete brachial valve; BB 95558	–	–

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. The distinctive paired dorsal septa, combined with the presence of a ventral spondylium simplex and characteristic external ornamentation, confirms that the Tourmakeady specimens are representatives of the clarkellid genus *Syntrophina*. Among described species of this genus, the Irish material most strongly resembles *Syntrophina nana* Ulrich & Cooper (1938: 223) from the Lower Ordovician of Colorado and Nevada. However, the latter species differs in being smaller, and in having a sharply folded sulcus rather than the broadly rectangular sulcus characteristic of the new Irish species.

Syntrophina magna is the largest brachiopod in the Tourmakeady fauna, and indeed these specimens are amongst the largest ever assigned to this genus.

Family **PORAMBONITIDAE** Davidson, 1853

Genus ***PORAMBONITES*** Pander, 1830

Porambonites dubius sp. nov.

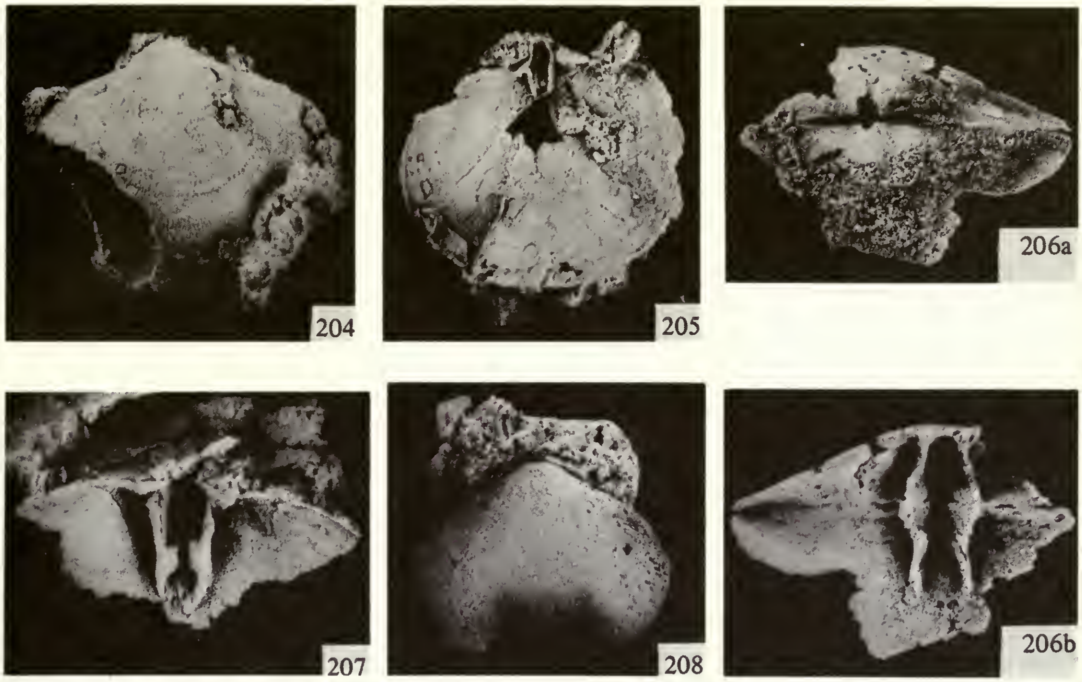
Figs 204–208

DIAGNOSIS. Medium-sized, elongately semi-elliptical to subtriangular *Porambonites*; pedicle valve moderately convex, averaging 83% as long as wide and 30% as deep as long; brachial valve moderately convex, averaging 82% as long as wide and 27% as deep as long.

NAME. 'Problematical'.

DESCRIPTION. Medium-sized, elongately semi-elliptical to subtriangular *Porambonites*; pedicle valve moderately convex, averaging 83% as long as wide (range 79–91%; n = 3) and 30% as deep as long (range 27–32%; n = 3), with a broad rectangular sulcus developed anteromedially; brachial valve moderately convex, 78% and 85% as long as wide and 24% and 29% as deep as long in two specimens, lateral margins of both valves strongly and smoothly rounded, anterior margin smoothly rounded with prominent, broad, median uniplication; external shell surfaces with faint, fine, pitted, radial ornamentation; ventral interarea short, very narrow, gently curved, apsacline, delthyrium open; dorsal interarea short, very narrow, anacline, notothyrium open.

Ventral interior with short, small, triangular teeth supported by well-developed dental



Figs 204–208 *Porambonites dubius* sp. nov. Fig. 204, **holotype** BB 95560, ventral view of conjoined valves, ×3; Fig. 205, paratype BB 95561, interior of incomplete pedicle valve, ×3; Fig. 206a, b, paratype BB 95562, posterior and anterior views of incomplete conjoined valves, both ×4; Fig. 207, paratype BB 95565, interior of incomplete pedicle valve, ×3; Fig. 208, paratype BB 95563, exterior of incomplete pedicle valve, ×2.

plates, parallel posteriorly but converging slightly anteriorly, inner flanks of dental plates thickened anteriorly to form paired, rectangular, subparallel bosses of shell.

Dorsal interior with short brachiophores flanked by small, shallow, sockets and supported by strong, parallel brachiophore bases becoming convergent anteriorly.

HOLOTYPE. Conjoined valves; BB 95560a, b: length 13·8 mm, width 15·1 mm. Fig. 204.

PARATYPES. Incomplete conjoined valves, BB 95562a, b, 95564a, b; incomplete pedicle valves, BB 95561, 95563 (width 15·4 mm), 95565.

TYPE HORIZON AND LOCALITY. Loc. 1.

DISCUSSION. *Porambonites* is a problematical taxon, the genus having been subject to considerable subdivision, usually without formal status, in an attempt to justify the inclusion of species displaying great morphological variability. In other brachiopod groups such variability has led to the erection of a number of genera, but the poor preservation and incomplete nature of much of the material on which the *Porambonites* species have been based militate against such taxonomic recognition. In as much as the present Tourmakeady specimens are characterized by a faintly pitted external ornamentation and by long, parallel, dental plates and brachiophore bases, they display the chief morphological characters of the genus *Porambonites*, to which they are accordingly assigned.

The Irish species can readily be distinguished from the majority of previously-published species of *Porambonites* by its unusually fine external ornamentation. *Porambonites*? sp. 2 from the Middle Ordovician of Newfoundland (Cooper 1956: 610; now assigned to a new genus *Cuparius* Ross, 1971) has a similar ornamentation, but differs from the Irish specimens both in outline (being subhexagonal with the maximum width anteriorly) and in the early, posterior, initiation of a sulcus which is only developed in the anterior portions of the Irish shells. *P. reticulatus* (Pander), from the Middle Ordovician of Russia, differs from the Irish species in outline, in having stronger ornamentation and deeper, wider, sulcation, and in being much more strongly biconvex in lateral profile.

Internally, illustrated specimens of *Cuparius*, including the Newfoundland specimens, have a well-defined, sessile spondylium, a feature lacking in the Irish specimens. Furthermore, *P. dubius* has much stronger brachiophore bases than *C. cardilatus* Ross (1971: 125), the type species of *Cuparius* from the Middle Ordovician of Nevada. On balance, therefore, the Irish material, although largely fragmentary, is sufficiently distinct and abundant to warrant specific recognition.

Family **CAMERELLIDAE** Hall & Clarke, 1894

Subfamily **CAMERELLINAE** Hall & Clarke, 1894

Genus ***IDIOSTROPHIA*** Ulrich & Cooper, 1936

Idiostrophia costata Ulrich & Cooper

Figs 209–214

DIAGNOSIS. Medium-sized, transversely to elongately subtriangular *Idiostrophia*, conjoined valves averaging 97% as long as wide and 58% as deep as long, external shell surfaces coarsely costellate with 7–12 angular ribs anteriorly.

DESCRIPTION. Medium-sized, transversely to elongately subtriangular *Idiostrophia*, conjoined valves averaging 97% as long as wide ($\bar{l}$ mm (var l) 6·33 (2·50), $\bar{w}$ mm (var w) 6·54 (2·98), r = 0·761; n = 42) and 58% as deep as long ($\bar{l}$ mm (var l) 6·49 (2·37), $\overline{th}$ mm (var th) 3·75 (1·11), r = 0·818; n = 37), lateral margins of both valves planar, tapering posteriorly, strongly compressed to form flattened, geniculate area posterolaterally, anterior margin moderately to slightly curved, rectimarginate; external shell surfaces with coarsely costellate ornamentation developed anteriorly with 7, 8, 10 and 12 angular ribs on 1, 7, 6 and 1 adult shells respectively.

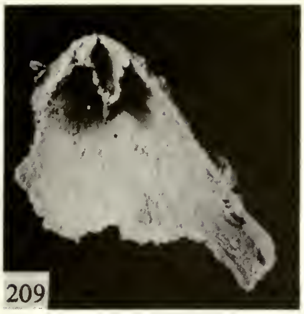
Ventral interior with small, triangular teeth supported by well-developed dental plates converging medially and uniting to form tongue-shaped, strongly elevated, concave spondylium supported by short, thin, tall, median ridge.

Dorsal interior with strong brachiophore bases united medially with long, low, median septum.

		length	width (mm)
FIGURED MATERIAL.	Conjoined valves; BB 95566a, b	9·6	7·2
	Conjoined valves; BB 95567a, b	6·6	6·7
	Conjoined valves; BB 95568a, b	6·6	5·7
	Conjoined valves; BB 95569a, b	7·3	5·9
	Conjoined valves; BB 95571a, b	5·0	5·0
	Incomplete pedicle valve; BB 95570	–	–
	Incomplete brachial valve; BB 95572	–	–
	Incomplete brachial valve; BB 95573	–	–

All Loc. 1.

DISCUSSION. *Idiostrophia* is a thin-shelled genus, and none of the Tourmakeady representatives is preserved whole. Indeed the bulk of the available sample consists of internal casts of conjoined valves from which most of the original shell material has been removed. However, a few fragments show characteristic camerellin internal morphology, and the casts have the flattened margins posterolaterally and triangular shape diagnostic of the genus *Idiostrophia*.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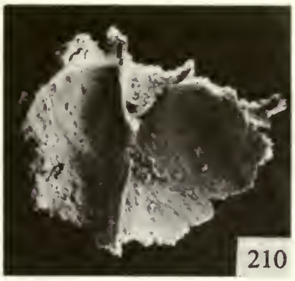
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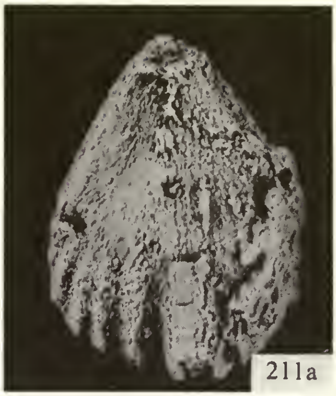
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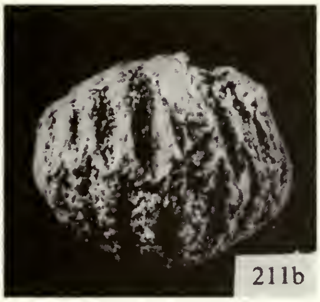
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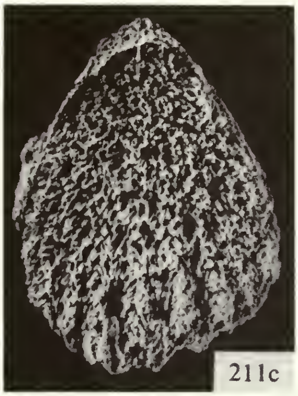
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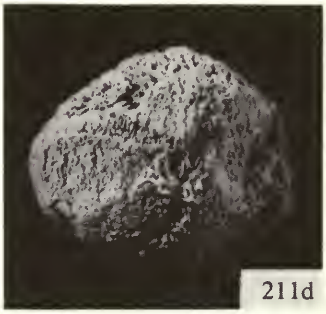
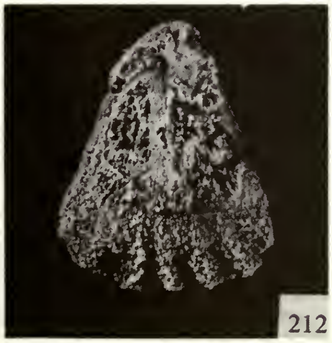

211d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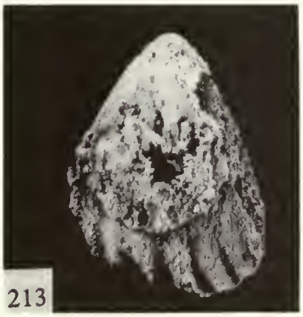
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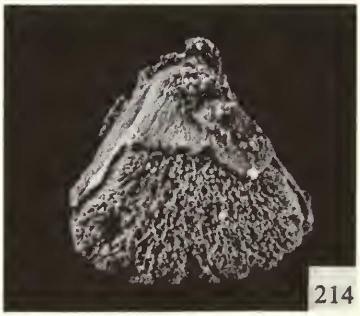
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Figs 209–214 *Idiostrophia costata* Ulrich & Cooper. Fig. 209, BB 95570, interior of incomplete pedicle valve, ×5; Fig. 210, BB 95573, interior of incomplete brachial valve, ×11; Fig. 211a, b, c, d, BB 95566, conjoined valves: a, dorsal view, ×5; b, anterior view, ×5; c, ventral view, ×5; d, posterior view, ×5; Fig. 212, BB 95569, conjoined valves, ×5; Fig. 213, BB 95568, conjoined valves, ×5; Fig. 214, BB 95567, conjoined valves, ×5.

Idiostrophia is known predominantly from conjoined valves, and few authors have been able to figure the internal morphology adequately. Consequently, much of the taxonomic differentiation at the species level has depended upon shell shape and ribbing. However, Ross (1972: 23) sounded a salutary warning about the use of such criteria when he described from a single piece of limestone over 500 conjoined valves which displayed extremely variable shape and rib-counts. In effect, the sample yielded a complete gradation between a range of morphological features which, taken in isolation, would have defined at least 4 separate taxa. The shape of the Tourmakeady specimens is also very variable, with 40% of the conjoined valves being longer than wide, and the remainder wider than long. Such ratio variation, however, does not constitute valid grounds for subdividing the sample as the two variants are present throughout the size range of the sample. Statistical tests have, in addition, shown that such variability is not allometric. The number of ribs does, however, remain relatively constant throughout the sample. *I. costata* from the Lower Ordovician Mystic Conglomerate of Quebec (Ulrich & Cooper 1938: 250) has a similar rib count, and also resembles the Irish specimens in size and shape. The Irish specimens are consequently considered to be conspecific, at least until a comparison of internal morphology can be made.

Acknowledgements

A number of our colleagues kindly provided assistance during the course of this study, either by allowing us access to collections under their care, or by examining and commenting upon otherwise inaccessible specimens on our behalf. In this respect we should particularly like to thank Dr G. A. Cooper of the U.S. National Museum, Dr L. R. M. Cocks of the British Museum (Natural History), Professor A. J. Rowell of the University of Kansas, and Dr M. R. Bassett, Welsh National Museum. The work was funded by NERC Grant GR3/3934, which is gratefully acknowledged.

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Accepted for publication 26 March 1984

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An account of the Ordovician rocks of the Shelve Inlier in west Salop and part of north Powys

By the late W. F. Whittard, F.R.S. (Compiled by W. T. Dean)

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ISBN 0 565 07004 5
ISSN 0007–1471

British Museum (Natural History)
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Vol 38 No 5 pp 271–412

Issued 31 January 1985

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Growth and shell shape in Productacean Brachiopods

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Synopsis

The growth of strongly curved productaceans, including geniculate species, is considered both in cross section and in longitudinal section. The relationships of shell shape to dorsal valve geniculations and the pattern of spines is studied in *Overtonia fimbriata*. The importance of studying shell growth in three dimensions when making functional interpretations is stressed, and some general palaeoecological conclusions are derived.

The growth and shapes of productacean brachiopods have been described by many authors, for example Sarycheva (1949), Rudwick (1959), Williams & Rowell (1965), Brunton (1966, 1982) and Shiells (1968), but most of them considered the shell in two dimensions, and often showed only the median longitudinal section to illustrate their discussions. Other growth studies have concentrated on shell microstructures, e.g. Williams (1968, 1971), Brunton (1969) and McKinnon (1974), but seldom have growth studies presented a more three-dimensional picture by including discussion on the growth of the brachiopod in width as well as in length. In addition to considering changes in both the cross-sectional and longitudinal views of productaceans, some of the growth patterns are related to the growth of spines on one or both valves and some of these patterns may help in the interpretation of palaeoecology.

Most brachiopods grow by peripheral shell accretion. The expansion of the two valves is controlled by the directional growth of secretory epithelium, which commonly altered during ontogeny, and thus altered the shapes of individuals (Williams & Rowell 1965). However, among the productaceans there are some very curved species in which growth directions changed abruptly, leading to the development of well-differentiated ears, dorsal valve trails or marginal rims (Shiells 1968). As viewed in median section the growth of ventral valves in productaceans is planispiral, with dorsal valves assuming various strategies to maintain body size and a close fit of the commissure. Within the Productacea it is possible to identify two general shapes, with many special cases of each and a variety of intermediate forms.

The first case, exemplified by species of *Krotovia, Juresania, Echinoconchus* or *Gigantoproductus*, was probably the more primitive, having an open planoconvex to concavoconvex lateral profile in which the dorsal valve curves to meet the ventral valve close to its margin (Fig. 1). Viewed laterally, the ventral valves of these shells retain an open bowl-like shape in which the anterior margins continued to grown principally in an anterior direction. A special case within this non-geniculated group is seen in species of *Productina*, e.g. *P. margaritacea* (Phillips) and *P. pectinoides* (Phillips). In these shells the dorsal valve curves gently to the anterior margin (as seen in longitudinal section) only after having produced a sequence of lamellose trails throughout ontogeny. Prins (1968) has illustrated the numerous trails in an example of *P. pectinoides* from north-west Spain and Fig. 2 shows the trails, trapped in sediment, of *P. margaritacea* from north-west England.

The second case includes genera such as *Inflatia, Diaphragmus, Antiquatonia* or *Alitaria*, in which the dorsal valve geniculated abruptly against the ventral valve so that in adulthood the anterior regions of both valves were parallel to each other and formed a pair of trails

Bull. Br. Mus. nat. Hist. (Geol.) **38** (5): 273–281 Issued 31 January 1985

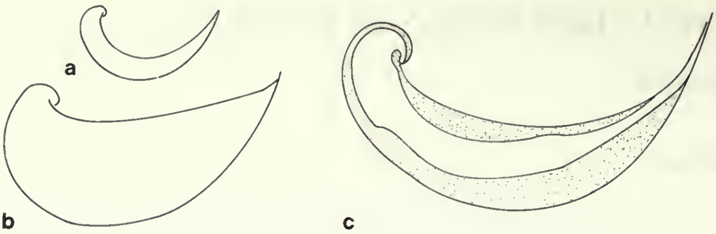


Fig. 1 Longitudinal sections of three non-geniculate productaceans, in which gently concave dorsal valves grew with the ventral valves in smooth curves. a – *Krotovia* sp.; b – *Echinoconchus* sp.; c – *Gigantoproductus* sp.

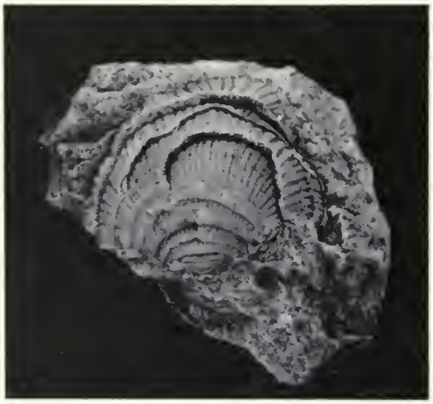


Fig. 2 *Productina margaritacea* (Phillips). The dorsal valve, exfoliated and viewed from the inner (ventral) side, showing a series of delicate lamellae extending at low angles into the surrounding limestone. The presence of these lamellae is why dorsal valve exteriors can seldom be cracked out of limestones. From the Viséan of the Clitheroe area of Lancashire. B336, × 1·5.

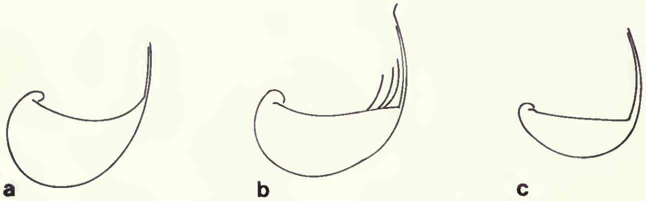


Fig. 3 Longitudinal sections of three productaceans with geniculated dorsal valves and well-developed trails. a – *Inflatia* sp.; b – *Diaphragmus* sp. in which the dorsal valve geniculated several times during growth; c – *Alitaria* sp.

(Fig. 3). In such shells the growth of the ventral valve, seen laterally, continued its expanding planispiral growth form so that its anterior margin grew increasing dorsally and may even have eventually overhung the dorsal valve.

In this discussion I use the terminology illustrated in Fig. 4, in which the term 'visceral cavity' includes the internal space occupied by the body and brachial cavities of the living animal. 'Lamellae' are surface shell ornamentations, some of which may have been trails at their time of growth at the valve margin. 'Trails' are developed only at the valve margins; they normally involve both valves and produce a narrow aperture. The term 'geniculation' is

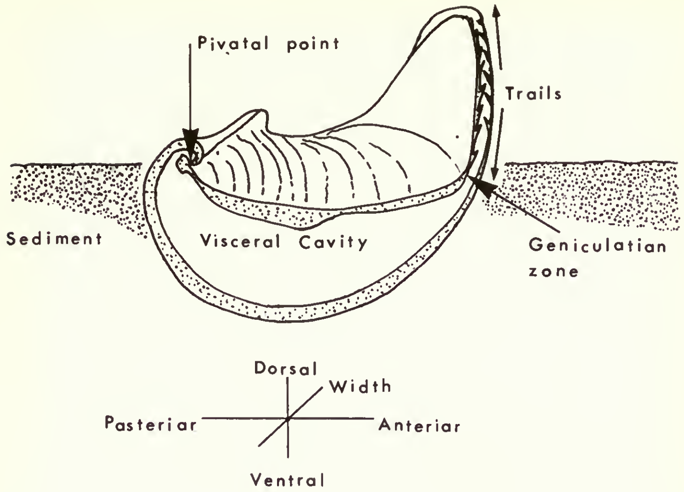


Fig. 4 Stylized longitudinal sagittal section of a productacean with a geniculated dorsal valve and well-developed trails. The pivotal 'point' is that about which the dorsal valve rotated when normally opening and closing, and also about which the valve hinged while increasing the depth of the visceral cavity.

restricted to abrupt angular changes in growth direction. Thus, other than in the growth of marginal rims or ears, where the geniculation is outwards, ventral valves in productaceans are not geniculate, but ventral valve geniculation is seen, for example, in leptaenids.

There is a problem in the increase of visceral cavity sizes in highly curved brachiopods, such as productaceans. Viewed in cross section, a brachiopod could only increase its visceral cavity width while the growing lateral margins continued to extend outwards (Fig. 5). Once the lateral margins had curved dorsally to the extent that they were parallel to each other (a full cross-sectional curve of 180°) it would then be impossible to widen the visceral cavity without a strong outward curve which, if followed by the dorsal valve, would produce a narrow trail-like rim. This type of growth is commonly seen in the posterolateral regions of productaceans in the formation of ears (Fig. 6). Ears are important morphological features for concavoconvex brachiopods such as productids or chonetids, because they provided the main posterior support for the dorsal valve (Fig. 7). Without ears the dorsal valve would have been pulled into the body cavity when the muscles contracted (see Brunton 1982). In

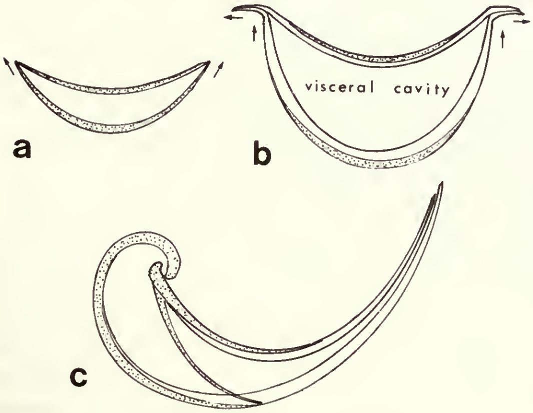
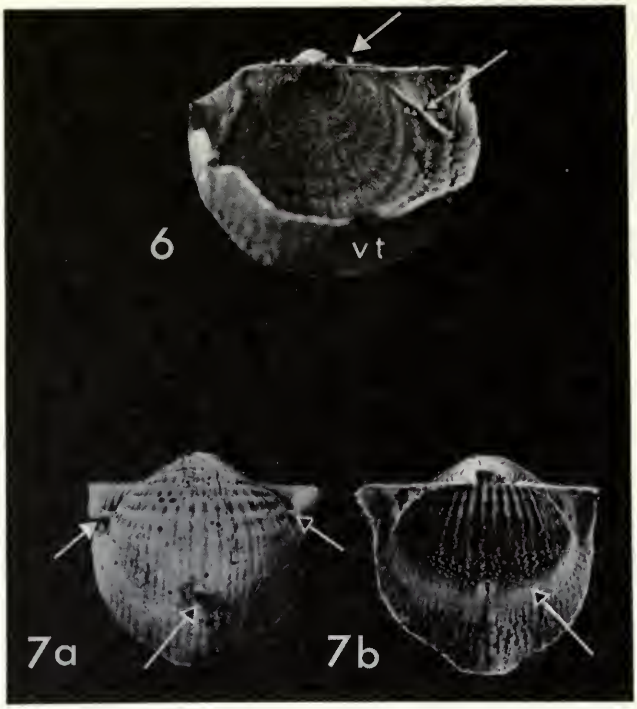


Fig. 5 Stylized cross sections of a productacean (a) when young, while growth of the valves continued to widen the visceral cavity, and (b) in adulthood, when it was impossible for the visceral cavity to increase its width. Increased width of the complete shell was achieved only by lateral geniculation of the ventral valve. (c), longitudinal section of a non-geniculated shell at the two stages of growth represented by (a) and (b).



Figs 6, 7 *Eomarginiferina trispina* Brunton, 1966, from the Viséan of Co. Fermanagh, Ireland, a species with well-developed ears formed by the lateral geniculation of part of the ventral valve margin. Fig. 6, anterodorsal view of an almost complete shell showing the clearly-defined ears providing support platforms for the dorsal valve; vt = ventral trail. The two arrows point to the stumps of juvenile clasping spines and to the dorsal valve ridge separating the viceral area from the ear. BB52890, × 4. Fig. 7, a ventral valve seen externally (7a) and internally (7b), showing the ears and positions of the three major spines (arrowed on 7a) which occur close to the place where the dorsal valve met the ventral valve; this smooth zone is arrowed on 7b. BB52893, × 3.

addition ears probably acted as stabilizers, preventing the posterior end of the productaceans from sinking too deeply into the sediment, and in some species they may have had a role to play in providing areas for gonadial tissues. However, the lateral growth of ears normally added significantly neither to the volume of the visceral cavity nor to its width, although they often added considerably to the maximum width of the whole shell.

The other alternative for widening the visceral cavity would be by shell resorption and redeposition. Resorption of shell material is well known in some brachiopods, such as in the loops of terebratulids or the growth of cyrtomatodont teeth. These are instances of modifications only to internal shell structures composed of secondary shell enveloped by epithelium. In no instance do we see natural resorption of the outer primary shell layer of brachiopods, other than perhaps for the unusual umbonal structure termed the ‘colleplex’ by Wright (1981), found in *Dictyonella* and *Isogramma*. (The increased size of the foramen of some older specimens of terebratulids should, I think, be explained entirely by shell abrasion.) The external ornamentation of brachiopods is determined by growth of the outermost primary shell layer, and had this been resorbed, to allow widening of the visceral cavity, the external ornamentation would have been destroyed, the new growth being differentiated by a discontinuity of ornament. Such breaks in ornament are only seen in specimens in which the shell has been damaged. Thus once the cross-sectional curve of the ventral valve had reached 180°, a U-shape, it became impossible to widen the internal visceral cavity. Depth could be increased by dorsal rotation from the hinge line of the dorsal valve, provided the anterior margins could be kept together (see the discussion on *Overtonia fimbriata* below).

This growth constraint means that if different individuals of a species grew to different widths in their U-shaped cross sections, perhaps at different stages in ontogeny, the ultimate adult widths of the specimens (not including ears) also varied. Growth, as seen in longitudinal sections, may have continued, producing a longer and dorsoventrally deeper specimen. In practice one finds some productacean species, apparently all fully grown and conspecific, in which the widths vary. This is especially true of the strongly curved dictyoclostids, antiquatonias and marginiferids. For instance, in a sample of silicified *Eomarginifera derbiensis* (Muir-Wood), specimens vary from 18 mm wide across the visceral region to 28 mm wide. Similarly, a sample of *Eomarginifera setosus* (Phillips) from one locality all appear to display adult characteristics, but vary from 12 mm to 19 mm in width, measured immediately in front of the ears.

As seen in longitudinal section, productaceans grew larger during late stages in ontogeny by following the growth patterns discussed above. The result of both growth patterns produced a commissure with trails, at least in adults. In the non-geniculate species the trails were shorter and more like narrow funnels widening inwards, but some, such as *Kochiproductus*, augmented the trail effect by producing externally-directed flanges (Shiells 1968). In a functional morphological study of *Levitusia* I (1982) discussed the advantage of trails to the living brachiopod. Many productaceans were adapted by shape, spine patterns and trails to live semi-infaunally on soft substrates. In such conditions, with much of the visceral region buried in sediment, long trails would have lifted the anterior and anterolateral commissure well above the sediment and allowed for the intake of cleaner water in the median sector. The gape of productaceans was commonly small, so the incurrent would have passed between two subparallel ciliated epithelial surfaces within a few millimetres of each other. Trails are normally strongly endospinous and these probably prevented larger particles from entering the brachial cavity. The ciliated epithelium probably assisted the flow of water and was able to reverse so as to expel unwanted particles, including faeces. Trails, therefore, were advantageous to most productaceans.

Recently, Lazarev (1981) discussed the ontogeny of productids with trails and showed a *Productus* sp. in longitudinal section at various growth stages. The dorsal series of trails developed at particular stages in ontogeny (the onset of which Lazarev suggested was sexual maturity), starting when the dorsal valve first geniculated against the ventral valve, and in his example this occurred at about half the full length of the shell. Lazarev commented that it was not clear why these dorsal trails had grown, although he suggested a brooding function for spaces between the dorsal trails. However, once a dorsal valve had fully geniculated to form a commissural trail, it would have been impossible for the visceral cavity to increase in size. To do so, the dorsal valve developed instead a succession of short dorsal trails, each separated by a brief period of normal anterior valve growth which maintained the basic valve profile. Thus, rapid geniculation and growth of the trail was followed by mantle regression to the pre-geniculation position and renewed normal forward growth to maintain a good commissural fit (Fig. 8a, b). As the dorsal valve grew forwards, it rotated slightly dorsally from the hinge and this increased the depth of the visceral cavity.

A good example of the intimate relationship between growth of the valves, their trails and lamellose surfaces, and with spines, is *Overtonia fimbriata* (J. de C. Sowerby) (Fig. 9). As seen in longitudinal section, the ventral valve grew in a regularly expanding spiral curve, but at regular intervals a series of concentric ridges, called rugae, were developed (Fig. 9). The dorsal valve grew almost flat, but with a series of short lamellae virtually perpendicular to the external surface, each of which had been a marginal trail for a short period (Fig. 9c). Spines grew from both valves. On the ventral valve more or less erect spines grew from the proximal slope of each ruga and recumbent spines from the slightly lamellose distal slopes: i.e. near the base of each depression between the rugae (Fig. 9d). Dorsal valve spines grew immediately after the growth of each upstanding lamella. As the ventral valve grew,

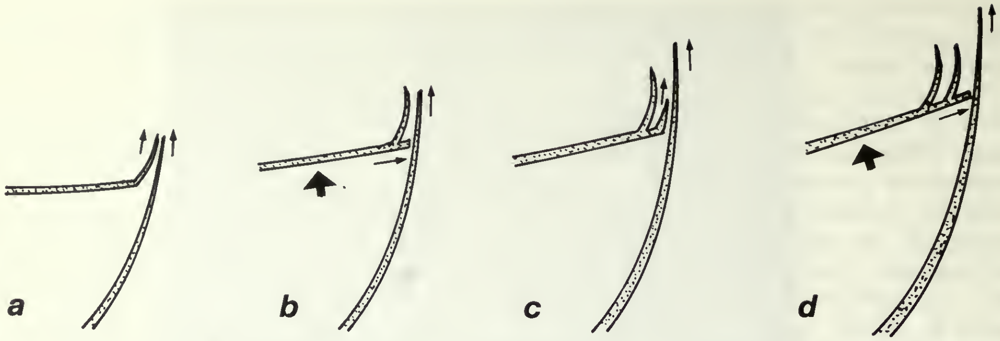


Fig. 8 Diagrammatic representation of growth at the anterior shell margin in a multi-geniculated species. (a), both valve margins growing anterodorsally. (b), dorsal valve rotating upwards anteriorly, increasing the visceral cavity depth, as its margin grows anteriorly against the ventral valve. (c), dorsal valve static, but its margin is geniculated and growing dorsally, parallel to the ventral valve. (d) as in (b).

increasing the distance between its margins and the umbo, the dorsal valve increased its length, while rotating slightly at the hinge to increase the visceral cavity depth. At the start of growth of each ventral valve concentric ruga, the dorsal valve margin grew, increasing the valve length and also budding a concentric band of spines. By the time growth had continued to the crest of the ruga, growth in the dorsal valve had altered, so that instead of expanding its dimensions it grew a short geniculated trail, as at positions A and C of Fig. 10. This maintained a close fit with the ventral valve while the distal side of the ruga grew in an arc retaining approximately the same distance from the pivotal point at the umbo. This pattern was repeated throughout growth of the shell, but with ever more closely spaced dorsal valve trails later in life, as the ventral valve ceased to add much to its straight line length from the umbo to its anterior margin. This diminution in the rate of spiral expansion also accounts for the flattening of the ridges on the ventral valve anteriorly, since less inward bend of the shell surface, at the distal side of the ruga, was necessary to allow for the non-expansion period of trail growth by the dorsal valve. In *O. fimbriata* two rows of differently orientated spines grew on each ventral ruga. The dorsal valve alternately extended its disc area, while growing a row of erect spines, and then produced the short high-angled trail (Fig. 9c). The ventral valve lamellae and recumbent spines correspond with the period of trail growth on the dorsal valve. Thus lamellae, involving mantle regression, were formed simultaneously on both valves. Had growth of the dorsal valve simply followed the margin of the ventral valve without geniculating, the disadvantages would have been both that there would have been no good commissural trail at any time during ontogeny, and also that the dorsal valve would have been strongly concave and similarly rugose, allowing no increase in the depth of the visceral cavity during growth, and producing an internal dorsal surface requiring much shell deposition to allow for the muscle and lophophore attachments.

While the North American *Fimbriaria* follows the growth pattern of *Overtonia* closely, the sparsely spinose, radially-ribbed linoproductid *Fluctuaria* from Europe had valve margins which grew together in a series of concentric ridges on both valves. However, the expansion rate of the growth curve is greater in *Fluctuaria* than in *Overtonia*, allowing the two valves to grow as they did. The ventral valve rugae of *Overtonia* may have resulted from the 'need' to grow a sequence of trails throughout life. Alternatively, or in addition, the concentric rugae may have been an adaptation to semi-infaunal burial in soft sediment; rugation is a common feature on the posterior regions of many productaceans. The continued development of spines throughout life might be taken as an indication either of deep burial in the sediment or of the spines having provided the open commissure with a wide-mesh protective grille.

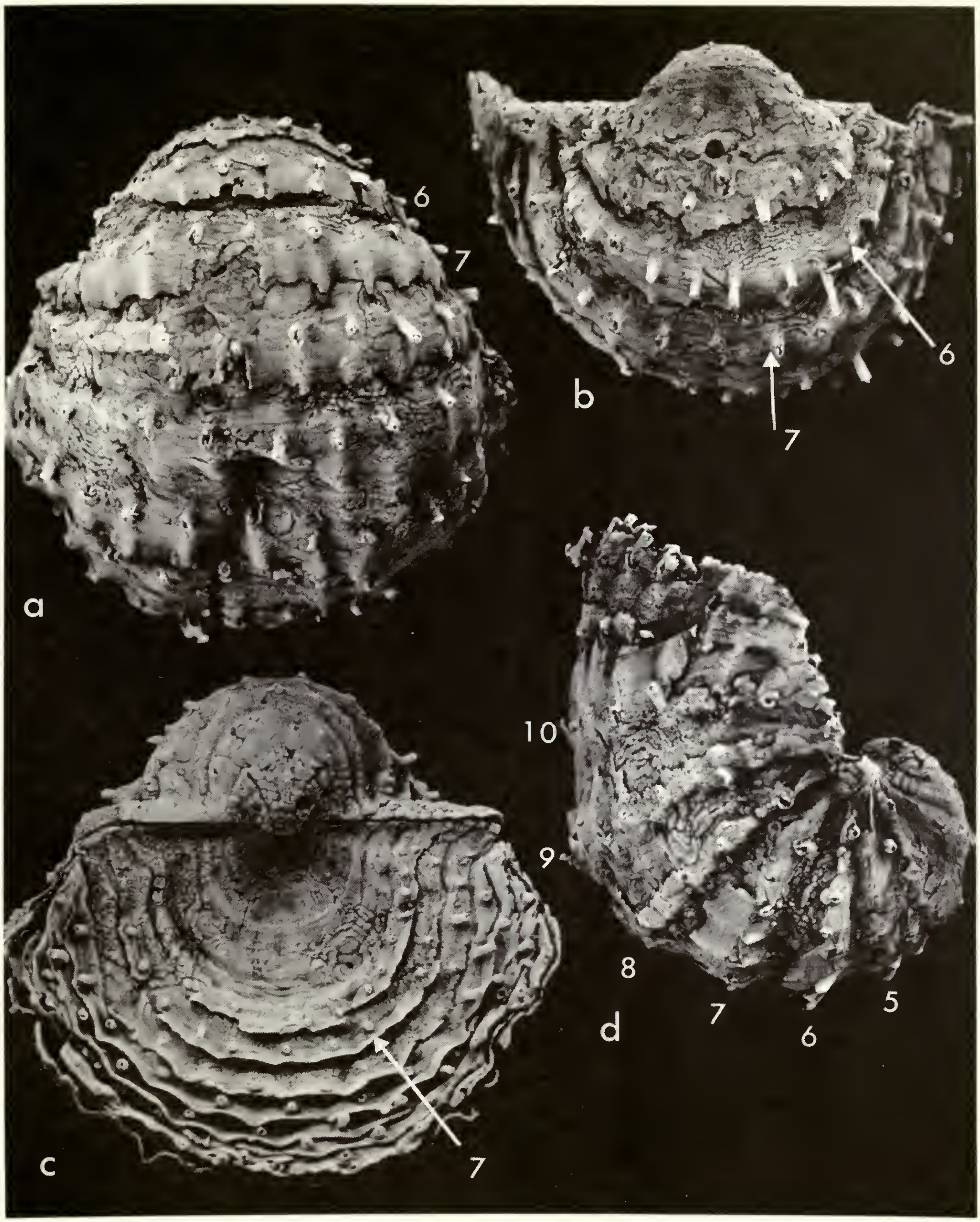


Fig. 9a–d *Overtonia fimbriata* (J. de C. Sowerby), a silicified specimen from the Lower Carboniferous, Asbian, of Co. Fermanagh, Ireland. The crests of rugae on the ventral valve have been numbered in such a way as to relate to those of Fig. 10, p. 280, but the two figures should not be taken as representations of the same specimen. The ruga numbered 7 grew at the same time as the lamella on the dorsal valve numbered 7 (Fig. 9c). The radial alignment of spines on every second row can be seen on both valves, for instance at the arrows marked 6 and 7. The recumbent lamellose spines (e.g. ruga 7 of Fig. 9a) can be seen projecting towards the gaps between the erect and recumbent spines of the next ruga. The specimen is seen in ventral view (a), posterior view (b), dorsal view (c) and lateral view (d). BB52845, × 4·5.

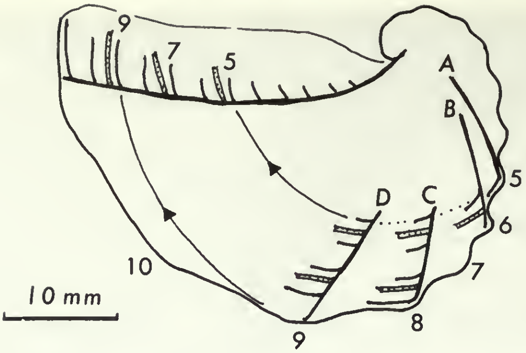


Fig. 10 Diagrammatic representation of *Overtonia fimbriata* in longitudinal section, showing the relationship of the dorsal valve, its lamellae and spines (finely stippled) with the ventral valve concentric rugae at several growth stages, A–D. For reference purposes the crests of four rugae are numbered 5, 6, 8 and 9. Dorsal valve lamellae started to grow when the valve margin was at the crests of these rugae, and the resulting lamellae (5–9) are marked. The rotations of points 5 and 9 on the dorsal valve are indicated, showing the movement from dorsal valve positions A to D, and to the adult position. Dorsal valve spines, on any one radial alignment, grew after the growth of every second lamella. Ventral valve spines (not illustrated) grew in similar alternating rows, but the two spines on a single ruga remained on the same radius so that the recumbent spines projected to the gap between spines on the next ruga anteriorly (see Fig. 9b).

The latter function may have been served by the distal recumbent spines of each ruga, which extended anteriorly beyond the valve margin.

Many productaceans, such as *Plicatifera*, most marginiferids, *Antiquatonia* and *Costiferina* grew large straight spines in distinctive patterns on their ventral valves late in life, after a period when small spines grew scattered over their more posterior regions. The large straight spines are not normally found very close to the ventral valve margins of adult shells, but some distance back, commonly in positions more or less where the dorsal valve meets or geniculates against the ventral valve (Fig. 7b, p. 276). If specimens are orientated so that a line through the umbo and the anteriormost large spines is horizontal, this probably approximates to the attitude of the specimen on or in the substrate, with the spines protruding close to the sediment surface. Before assuming its final adult position, the shell must have retained a favourable position during growth by a rotational sinking of the anterior part of the shell relative to the umbo. Without this rotational movement the shell would have grown with its adult trail overhanging the umbo, or even with its trail and commissure resting on the sediment posteriorly – a position in which survival would not have been possible.

Species having valves more or less covered by spines tend to have finer spines, commonly extending to the valve margins: such are productellids, overtoniids, echinoconchids and some buxtoniids. Some representatives of these taxa probably used their spines to entangle in clusters, but many do not have strong curvature with long trails, and these probably lived semi-infaunally with much of the shell below the surface of a soft sediment. Species with a proliferation of fine spines on both valves extending right to the margins probably gained protection at the gape against small organisms entering the shell, since the spines would have partially interdigitated across the commissure.

Much of the proliferation of productaceans during the Carboniferous period was probably in response to the development of strategies to cope with living on soft bottoms. By contrast, many strophalosiaceans and aulostegaceans are characterized by morphologies showing adaptations to life on hard surfaces, commonly in varied reef environments. Cementation early in life or throughout life, and spines capable of entangling or fixing to hard surfaces or of growing around hard objects, are yet other modes of life. While strophalosiaceans had their origins in the early Devonian and continued through the Carboniferous in the relatively rare reef environments, it was in the Permian, at a time when hardgrounds and reefs were commoner, that strophalosiaceans and aulostegaceans flourished most abundantly. The taxonomic relationships of these groups might be clarified by treating aulostegaceans as productaceans specialized to life on hard substrates.

Acknowledgements

I thank Dr L. R. M. Cocks for constructive criticism of an early draft of this paper and Dr D. J. C. Mundy for helpful discussions on some aspects of growth in brachiopods.

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Palaeosiphonium, a problematic Jurassic alga

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Synopsis

'Pseudocodium' convolvens Praturlon 1964, a problematic Tethyan Jurassic alga, is re-examined from English materials and interpreted from its structure as very probably an extinct member of the 'siphonous Chlorophycophyta', but a family assignment is not attempted. The name *Pseudocodium* being preoccupied by a living alga, the fossil is renamed *Palaeosiphonium*. Distribution and range are summarized: it is both Tethyan and extra-Tethyan geographically, and Upper Bathonian to bottom Callovian stratigraphically.

Introduction

The problematic microfossil discussed here was described by Praturlon (1964) from the Jurassic (Upper Dogger or Malm) of central Italy. He regarded it as algal, though peculiar in structure, and named the species *Pseudocodium convolvens*. Farinacci & Radoičić (1964: pl. 6) and Radoičić (1966: pl. 8) recorded the species from the Upper Bathonian–bottom Callovian of Jugoslavia. Praturlon (1966) recognized that the generic name *Pseudocodium* was preoccupied by a Recent alga (*Pseudocodium* Weber van Bosse 1896), but in view of the taxonomic uncertainty over the fossil, he did not rename it. Elliott (1975) recorded it from the Upper Bathonian of England, where it is a rare fossil, and drew attention to an alga figured by Hudson (1970) from the Middle Jurassic of Scotland, which showed some similarity although the evidence was too limited for a positive identification. Mišik (1979) listed Praturlon's species from Czechoslovakia, in a remanié pebble found in the Cretaceous.

A further find in England provides the occasion for a fresh evaluation of this organism, and the opportunity is taken to rename it.

The figured material is in the Department of Palaeontology, British Museum (Natural History). Figs 1–4.

Description

PALAEOSIPHONIUM, nom. nov.

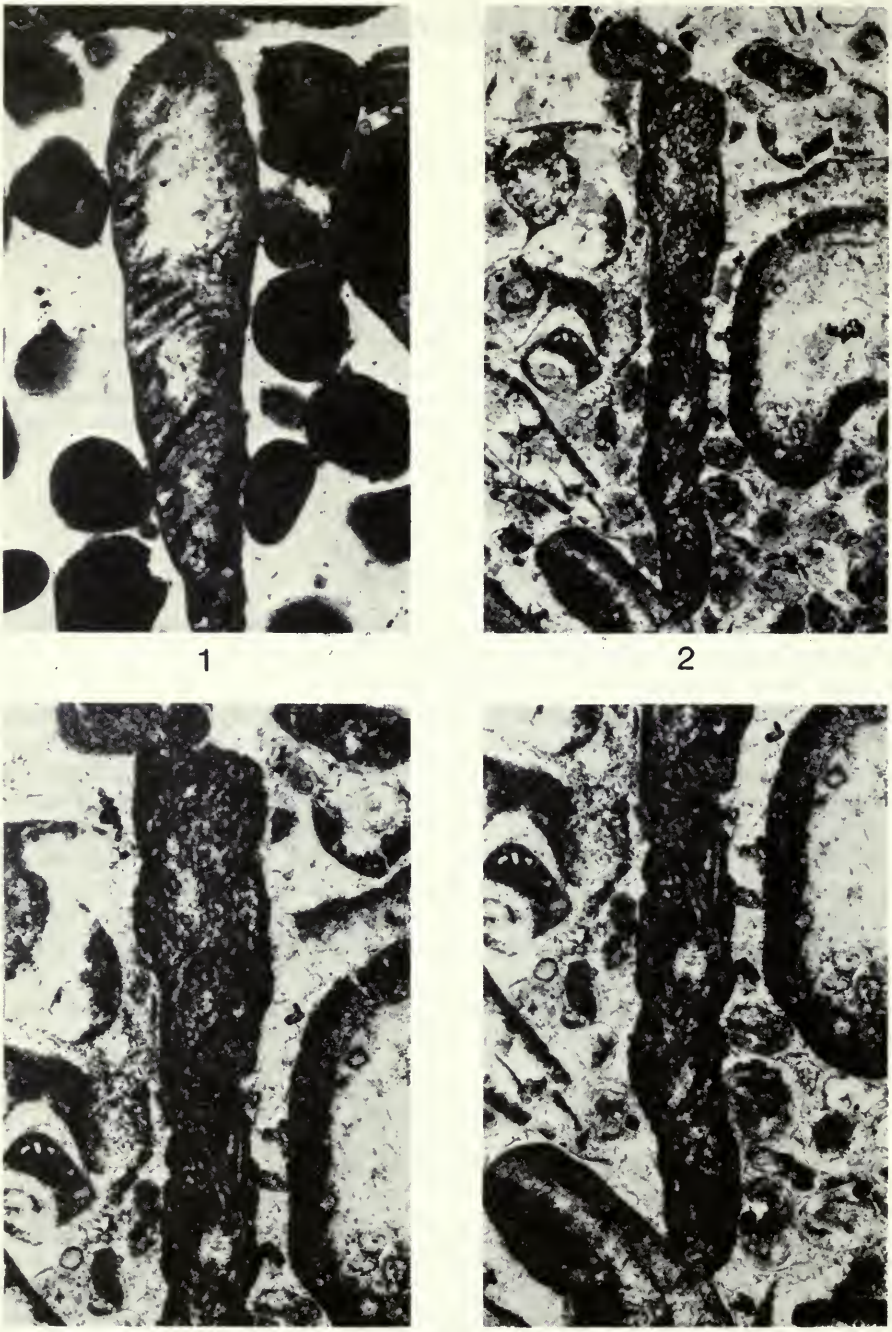
[= *Pseudocodium* Praturlon 1964, *non* Weber van Bosse 1896]

Generic diagnosis. Elongate slender cylindrical or subfusiform calcareous bodies, showing irregular external constrictions of diameter. Central medullary zone with tendency to recrystallization, main medullary zone showing a longitudinally directed tangle of apparently tubular threads, very confused subperipherally, where it is possible that they may branch and anastomose, but without marked diameter diminution. The whole complex is enclosed by a single subdermal tubular thread, which winds spirally from end to end of the body, without communicating throughout its main length with the inner complex. Calcification moderately heavy, completely enclosing these structures.

Type species. *Palaeosiphonium convolvens* (Praturlon) Elliott.

Discussion. This curious fossil was described in detail in Praturlon's original account (1964); he was careful to give a factual account separate from interpretation. The medullary

Issued 31 January 1985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Figs 1–4 *Palaeosiphonium convolvens* (Praturlon) Elliott. Middle Jurassic, Upper Bathonian, Hodsoni Zone; Cirencester area, Gloucestershire, England. Fig. 1, longitudinal–tangential section showing outer spiral. V57651, × 30; Daglingworth Quarry. Fig. 2, longitudinal section showing medullary thread-system in various aspects, due to plane of section cutting irregularities of unit. Outer spiral mostly missing due to worn state of unit. V62034, × 18; Fowler's Hill, Quenington. Figs 3, 4, portions of specimen seen in Fig. 2, × 27, to show detail.

structure could be one of many variants of that found in the serial-segmented Udoteaceae (Codiaceae auctt.), and in a general way recalls *Arabicodium* or *Palaeoporella*. The outer spiral is however quite anomalous for this group. Inevitably it brings to mind the spiral structures seen in the Charophyta, particularly those of the calcified reproductive bodies ('oogonia'). However, these spirals develop from several cells each originating its own spiral curve, and the result is not a single spiral. The internodal spirals of the Jurassic *Echinochara* are also multiple in origin. *Palaeosiphonium* cannot in any way be homologized with the Charophyta. Praturlon believed his fossil to be algal, with which I agree, but he left it *incertae sedis*.

If one considers the gross morphology of various living genera of 'siphonous' green algae, irrespective of their allocation in detailed higher classification, which is based on all evidence including cell-structure and biochemistry not available in fossils, there exists a considerable variety of general form and structure. *Ernodesmis* shows clusters of branches; *Udotea* shows a fan formed of coarse longitudinal threads bound together by subsidiary laterals, while in *Anadyomene* the fan is formed of large, dividing longitudinal elements, intersticed closely with tiny laterals. *Penicillus* shows a stalked tufted head of beaded longitudinals, *Chamaedoris* a stalked cup of felted threads, and the familiar *Halimeda*, with medullary longitudinals and dividing cortical utricles, typifies the serial-segmented pattern.

I suggest that *Palaeosiphonium* is yet another variant. The remains as found (probably serial-segments but just possibly single individuals), would not calcify until fully or almost fully grown, as in *Halimeda*. In the green, growing phase the threads would have proliferated as a tangled longitudinal bundle, but with one thread individualized on an outer, spiral, course. Irregularities in growth would lead to its occasionally constricting the loose, growing structure, and this would be correlated with the absence of a mass of peripheral utricles as in the advanced *Halimeda*. Eventually the structure would have calcified, giving the remains found fossil.

Detailed serial sections of the terminations of exceptionally well-preserved examples are necessary to check the genesis and termination of the spiral, and suitable material is not available to me. But this explanation seems the most likely. If it is correct, then the extinct *Palaeosiphonium* is certainly a green alga within the 'siphonous Chlorophycophyta complex' (Egerod 1952). Family allocation is nearly impossible, however, unless the view is taken that it should be made the type of a new monogeneric family. The biological details available for the living taxa, and used in various classifications, are much greater than those to be seen in the fossil, and in this case the similarities are insufficient for other than a very general allocation.

Geological age of *Palaeosiphonium*

The two English examples which led to this restudy are slightly smaller in unit- and thread-dimensions than the type material, but otherwise they correspond. They come from localities about 15 km apart near Cirencester, Gloucestershire, southern England. The algal level at one locality, Daglingworth, can be dated on ammonite evidence as referable to the Hodsoni Zone of the Upper Bathonian (Torrens, *in* Cope *et al.* 1980: 35). The algal level at the other locality seems to be in the same stratigraphic position; at both localities *Palaeosiphonium* is accompanied by the algae *Dobunniella coriniensis* Elliott, *Sarfatiella dubari* Conrad & Peybernès, *Pycnoporidium* sp., *Solenopora jurassica* Brown and various cyanophytes. In the same mid-Cotswold region the well-known *Solenopora* occurrences of Foss Cross quarry (Harland & Torrens 1982) and the adjacent railway-cutting are also at this approximate level.

Taken in conjunction with the Mediterranean occurrences, *Palaeosiphonium* seems to occur in the upper part of the Middle Jurassic (Upper Bathonian–bottom Callovian). In geographical distribution it is both Tethyan and extra-Tethyan (Elliott 1977), though rare in the latter. Reasons for this distribution in other tropical algae have been discussed by me recently (Elliott, in press).

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Upper Ordovician brachiopods and trilobites from the Clashford House Formation, near Herbertstown, Co. Meath, Ireland

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Synopsis

Brachiopods and trilobites are described for the first time from the Clashford House Formation, Co. Meath. The fauna comprises the brachiopods *Hibernodonta praeco* gen. et sp. nov. (a new genus of stropheodontid), *Plaesiomys* cf. *multiplicata, Oanduporella* cf. *reticulata, Sericoidea* cf. *abdita, Kiaeromena* sp. together with an indeterminate craniid and orthid, and the trilobites *Deacybele* aff. *arenosa, Harpidella*? sp., *Gravicalymene* sp., *Miraspis* sp. and an indeterminate lichid. The assemblage indicates a late Ordovician (Caradoc) age for the formation and probably inhabited the shelves and slopes of a volcanic archipelago seaward of the Anglo-Welsh and Irish Sea areas.

Introduction

The fauna described in this paper was collected from a small outcrop on the west bank of the River Delvin in the townland of Naul, Co. Meath. The locality lies approximately 880 m north-east of Naul, which is situated some 7·5 km SSW of Balbriggan, Co. Dublin (Romano 1980*b*; Fig. 1 herein). The area had received scant attention since the explanatory Memoir of 1871 (Hull & Cruise) until Romano (1970, 1980*b*) revised the succession and recognized the presence of probable Ordovician rocks.

The fossiliferous outcrop is assigned to the Clashford House Formation (Romano 1980*b*), a unit which underlies a dominantly volcanic sequence of tuffs and lavas showing close petrographical similarity to the volcanic rocks of Balbriggan farther east (France 1967). Shelly faunas also occur at Balbriggan and, from France's interpretation of the structure of the area, are from mudstones underlying the volcanic rocks.

The Clashford House Formation consists of cleaved grey mudstones with rare silty bands. The mudstones are typically rather blocky and homogeneous; lamination and banding only occur where the beds become more silty. On the basis of a sparse fauna, Mitchell (*in* Romano 1980*b*: 206) suggested that the brachiopods indicated a late Ordovician, possibly early Ashgill age. The acritarchs recovered from the sample proved inconclusive. Further collections by D. A. T. Harper & W. I. Mitchell have now yielded a much richer fauna which provides the basis for the present paper.

Bull. Br. Mus. nat. Hist. (Geol.) **38** (5): 287–308

Issued 31 January 1985

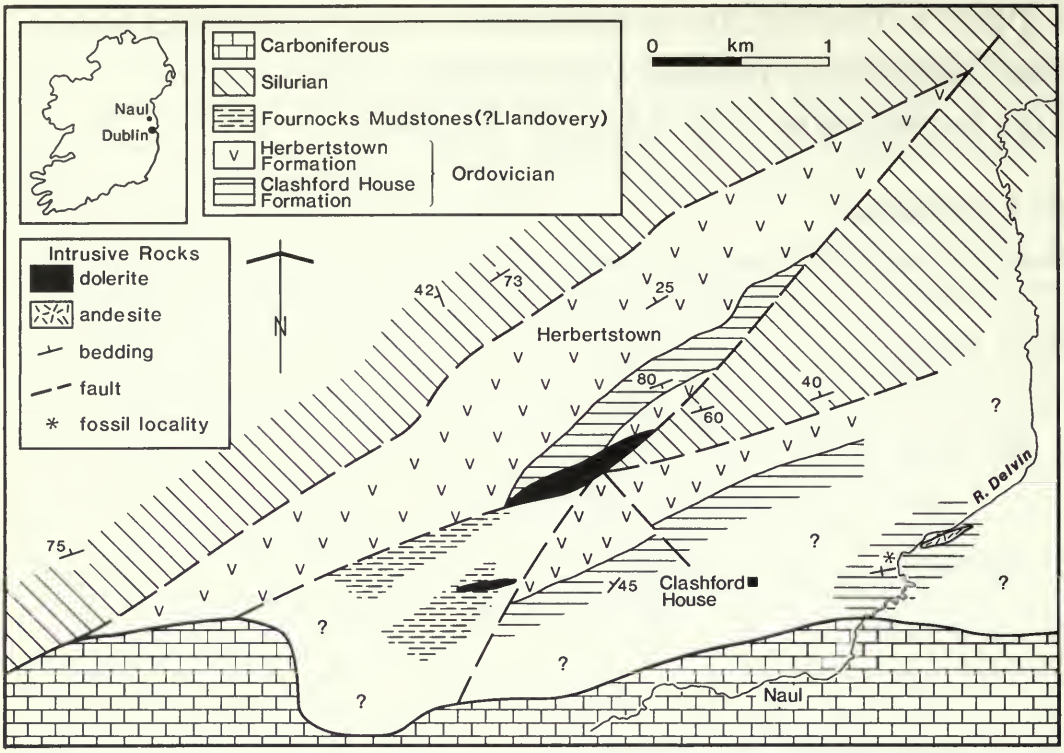

Naul
Dublin
Carboniferous
Silurian
Fournocks Mudstones(?Llandovery)
Herbertstown Formation
Clashford House Formation
Ordovician
0 km 1
Intrusive Rocks
dolerite
andesite
bedding
fault
fossil locality
N
42
73
25
Herbertstown
80
60
40
75
45
Clashford House
R. Delvin
Naul
?

Fig. 1 Simplified geological map of the Herbertstown area (after Romano 1980*b*: fig. 1) showing the fossil locality mentioned in the text. The Silurian rocks, apart from the Fournocks Mudstones, belong to the Skerries Formation of *lundgreni* Zone age (late Wenlock) or younger (Rickards *et al.* 1973).

The general area from which the material was collected was referred to as the Herbertstown area by Romano (1980*b*), since it is in this townland that the volcanic rocks in particular are best exposed. For convenience, the material described here is known as the Herbertstown fauna.

All type and figured material has been given to the British Museum (Natural History) (Brachiopods BC.9171–9197; Trilobites It.17040–17051); a selection of comparative material is in the Ulster Museum, Belfast.

The systematic palaeontology of the Brachiopoda is by D. A. T. Harper & W. I. Mitchell, and of the Trilobita by A. W. Owen & M. Romano.

Correlation and environmental setting

In a preliminary assessment of the age of the Clashford House Formation, Romano (1980*b*: 208) considered the unit to correlate with the Caradoc/Ashgill on the basis of very limited palaeontological evidence. The new collections provide a more precise age for these strata.

Although none of the Herbertstown brachiopods is unequivocally assigned to established species, three, *Plaesiomys* cf. *multiplicata*, *Oanduporella* cf. *reticulata* and *Sericoidea* cf. *abdita*, are sufficiently similar to the named species to permit a tentative correlation of the Clashford House Formation with sequences elsewhere. The genus *Oanduporella* Hints is typical of a restricted facies in the Oandu Stage of the east Baltic; the type species, with which the Irish specimens are compared, has been recorded from the 'Oandu Member' of the Oandu Stage of northern Estonia and the Oandu Stage of south-east Estonia and Lithuania (Hints 1975: 105). Both horizons are upper Caradoc (probably high Marshbrookian to low Onnian) equivalents. But since the precise range of only the type species is known with certainty, in Estonia and Lithuania, the use of *Oanduporella* for accurate correlation is at present limited. *P. multiplicata* is from high Soudleyan strata at Glyn Ceiriog. Since *Sericoidea abdita* Williams was initially described from the Derfel Limestone (Costonian) of north Wales, forms approximating to it have been described from the Balclatchie Mudstones (low Caradoc; Ingham 1978: 167) of the Girvan district, the Hagley Shales (Soudleyan) of the Shelve inlier (Williams 1974: 139) and the Tandinas Shales (Costonian) on Anglesey (Bates 1968: 173). The other elements of the brachiopod fauna, with the exception of *Hibernodonta praeco*, indicate, on balance, a middle Caradoc (Soudleyan–Longvillian) age for the Clashford House Formation.

Of the trilobites, only the *Deacybele* provides any indication of the precise age of the Herbertstown fauna. Other forms ascribed to the genus are restricted to the Caradoc and lowest Ashgill (on the basis of current correlations), and if the suggested similarity to *D. arenosa* (M'Coy) is correct a Caradoc age is probable.

No comparable brachiopod faunas have yet been described from the Caradoc of eastern Ireland. However, farther east at Balbriggan, Mason (*in* France 1967: 291) identified a Longvillian fauna from, principally, mudstones associated with a sequence of basic-intermediate volcanic and volcaniclastic rocks. Romano (1980*b*: 212) considered the Balbriggan fauna to be from mudstones beneath the volcanic rocks and suggested a tentative correlation with the Clashford House Formation; the new palaeontological data presented herein confirms this. These data provide important constraints regarding the timing of volcanism in eastern Ireland.

Elsewhere in Ireland formations at Bellewstown, Grangegeeth, Rathdrum, Enniscorthy, Courtown and Tramore have been correlated with the middle Caradoc (Brenchley *et al.* 1977 and references therein; Carlisle 1979; Romano 1980*a*). To date, however, no brachiopod faunas similar to that from the Clashford House Formation have been recorded from these areas.

Table 1 Sample count of the brachiopod fauna of the Clashford House Formation. Abbreviations: PV – pedicle valves, BV – brachial valves, ? – indeterminate valves, BKN – broken valves. Only five conjoined pairs, all of *Oanduporella* cf. *reticulata*, were recovered during the present study; these are included in the sample count.

	PV	BV	?	BKN	Total	%
Craniid gen. et sp. indet.	1	–	–	–	1	1
Orthid gen. et sp. indet.	1	–	3	3	4	4
Plaesiomys cf. *multiplicata*	15	8	5	22	28	31
Oanduporella cf. *reticulata*	17	18	4	25	39	43
Sericoidea cf. *abdita*	6	2	–	4	8	9
Kiaeromena sp.	2	–	–	2	2	2
Hibernodonta praeco gen. et sp. nov.	2	3	4	5	9	10

Data on the abundance and breakage of the Herbertstown brachiopods are summarized in Table 1. Most of the brachiopod shells are slightly broken and disarticulated, as are all the trilobites. However, a wide individual size range is represented in the larger samples. The fauna comprises both pedunculate and non-pedunculate forms, whilst elements considered to be typical of shallow (*Plaesiomys*) and deep (*Sericoidea*) palaeocommunities in the Caradoc (Pickerill & Brenchley 1979; Hurst 1979; Lockley 1983) occur together. Romano (1980*b*:

214) suggested that the early Caradoc benthos of eastern Ireland may have occupied the shallow water shelves around volcanic centres. A similar environment for the Herbertstown fauna is envisaged, although it seems likely that it has been rapidly transported down-slope prior to final burial in deeper water on the unstable slopes of the volcanic islands.

The brachiopods are more similar to those of the Baltic and Anglo-Welsh provinces; they have little in common with coeval assemblages from the North American and Mediterranean provinces. A situation seaward of the Baltic and Anglo-Welsh plates at high to intermediate latitudes (see Cocks & Fortey 1982) is therefore suggested.

Systematic palaeontology: Brachiopoda

Although much of the material is well preserved it is largely broken and has suffered some tectonic deformation. Consequently statistics and precise measurements of variates are not available. However, fractions in words, based on the sample means of estimated values of given variates, are provided in the taxonomic descriptions as a rough guide to the relative dimensions of features of the shell. The terminology is that of Williams *et al.* (1965). Measurements may be made from the figures for which the given magnifications are accurate to within 5%. All figured specimens have been lightly coated with ammonium chloride sublimate and photographed in the conventional manner.

Specimens of *Plaesiomys* cf. *multiplicata* (Fig. 11) and *Kiaeromena* sp. (Figs 43–46) have been extensively bored; the borings will be described elsewhere as a separate part of this study.

Suborder **CRANIIDINA** Waagen, 1885

Superfamily **CRANIACEA** Schuchert, 1896

Family **CRANIIDAE** Menke, 1828

Craniid gen. et sp. indet.

Figs 2–3

Material. One virtually complete but poorly preserved valve.

Description. Small, convex valve of elongate subcircular outline, about as long as wide and about one-fifth as deep as long. Anterior and lateral profiles weakly convex with broad, shallow sulcus pronounced anteriorly; umbo subdued. Hinge line curved, about four-fifths maximum width which occurs at about mid-valve length. Ornament of very fine costellae, with about 20 per mm medially at the 2·5-mm growth stage; concentric growth lines variably accentuated with 4 per mm developed at anterior margin, where a feeble limbus is present.

Discussion. This small, poorly preserved valve is assigned with difficulty to the Craniidae largely on account of its shape and probable calcareous shell. Although there is little indication which valve the mould represents, the low convexity and submarginal umbo suggest the pedicle valve. Of the known genera of craniids it is most similar to *Orthisocrania*; it has a fine costellate ornament, a submarginal beak and a definite limbus. It is noteworthy that in his review of the distribution of *Orthisocrania* in the British Isles, Wright (1970: 101) considered it to be restricted to rocks of Longvillian age, although it may have arrived earlier, during for example the Soudleyan Stage (Wright 1970: 102). A more precise assignment of this specimen is clearly not warranted since the shell is small, probably immature and poorly preserved; moreover, information regarding the brachial valve and both valve interiors is lacking.

Suborder **ORTHIDINA** Schuchert & Cooper, 1932

Subfamily **ORTHACEA** Woodward, 1852

Family **ORTHIDAE** Woodward, 1852

Orthid gen. et sp. indet.
Figs 4–5

MATERIAL. One incomplete pedicle valve and a few fragments bearing a similar style of ornament.

DISCUSSION. The most complete valve is that figured; it is about as wide as long and about one-fifth as deep. The anterior profile is convex medially with flatly concave flanks and the lateral profile slopes gently anteriorly from the small convex ventral umbo. About 17 strong costae are present with fairly angular profiles and except the median costa all others appear to develop costellae by internal and external branching with the order as follows: $5a^-$, $4a^-$, $3a^\circ$, $2a^\circ$, $1a^-$. The earliest costella appears at the 3-mm growth stage. The median rib (unnumbered) has a wavelength of 0·75 mm at the 5-mm growth stage. A concentric ornament of well-defined growth lines, six per mm at the 5-mm growth stage medially, is developed. Although the valve has been slightly deformed the shape and ornament suggest inclusion within the genus *Nicolella* (Reed, 1917). The high number of costae and the early appearance of costellae by external and internal branching indicate a similarity to *N. humilis* Williams (*in* Whittington & Williams 1955: 405) from the Derfel Limestone (Costonian), rather than to stratigraphically younger forms assigned to *N. actoniae* (J. de C. Sowerby), s.l. (see Williams 1963: 352 and Cocks 1978: 41).

Family **PLAESIOMYIDAE** Schuchert, 1913

Subfamily **PLAESIOMYINAE** Schuchert, 1913

Genus ***PLAESIOMYS*** Hall & Clarke, 1892

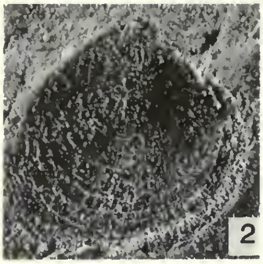
TYPE SPECIES. By original designation, *Orthis subquadrata* Hall, 1847, from the Richmond Group (upper Ordovician) of New York State, U.S.A.

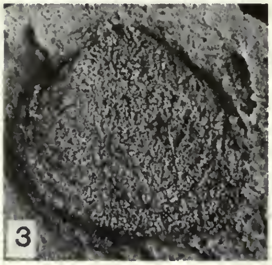
Plaesiomys cf. ***multiplicata*** Bancroft 1945
Figs 6–24

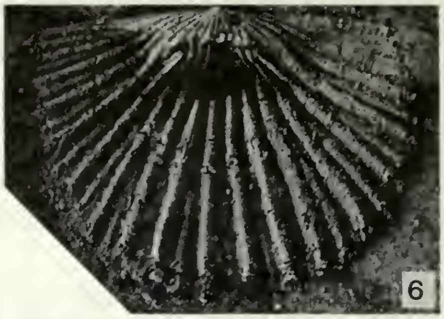
cf. 1945 *Dinorthis (Plaesiomys) multiplicata* Bancroft: 244; pl. 35, figs 4–6; pl. 36, figs 1–3.
cf. 1968 *Dinorthis multiplicata* Bancroft; Diggens & Romano: 47; pl. 5, fig. M.
cf. 1978 *Plaesiomys multifida* (Salter); Cocks: 50 (pars).
cf. 1978 *Dinorthis multiplicata* Bancroft; Brenchley: 160.
1980*b* *Lordorthis* sp.; Mitchell *in* Romano: 206.

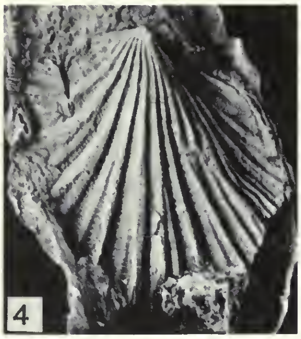
MATERIAL. Fifteen pedicle valves, eight brachial valves and five indeterminate valves.

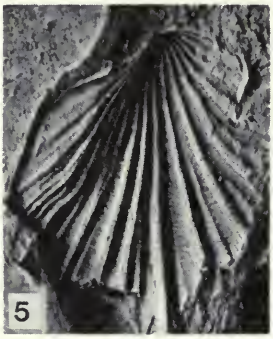
DESCRIPTION. Moderately large, dorsibiconvex to convexiplane valves of rounded subquadrate outline, with maximum width at between hinge line and one-third valve length; hinge width about four-fifths maximum width. Anterior commissure rectimarginate and cardinal extremities obtuse and rounded. Pedicle valve about three-quarters as long as wide and less than one-fifth as deep as long. Anterior profile with swollen axial surface posteriorly; elsewhere flanks and axial surface flat to weakly concave. Lateral profile feebly convex at and near fairly prominent umbo, elsewhere inclined gently anteriorly. Ventral interarea less than one-quarter valve length, flat and apsacline; delthyrium wide, open and rarely with indications of minute, subcircular, apical pedicle foramen. Brachial valve evenly convex in both profiles, about seven-eighths as long as wide; dorsal interarea short, flat and anacline with wide, open notothyrium. Radial ornament of subangular to evenly rounded costae,

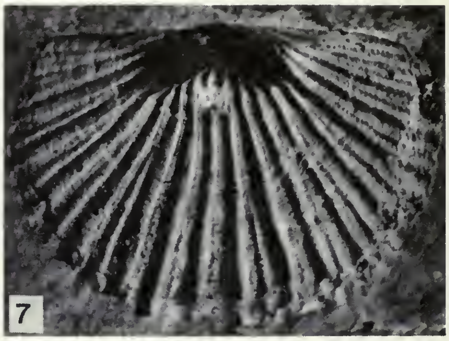


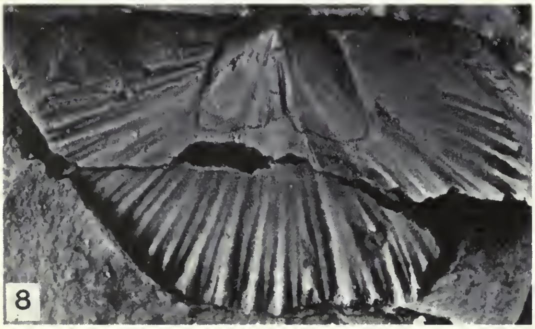


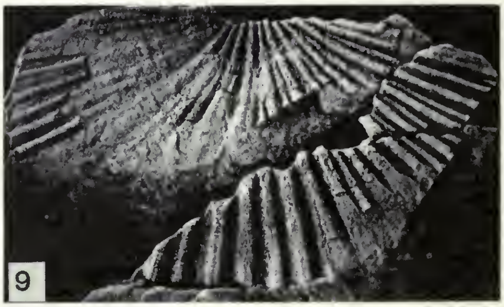


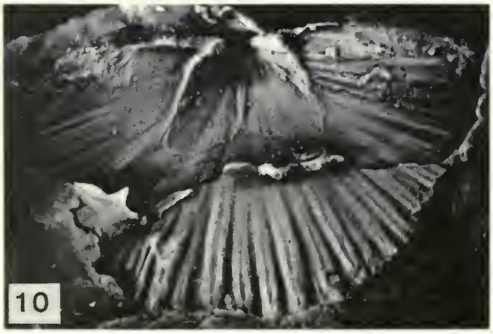


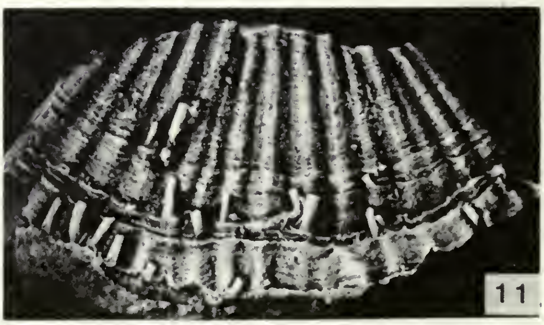








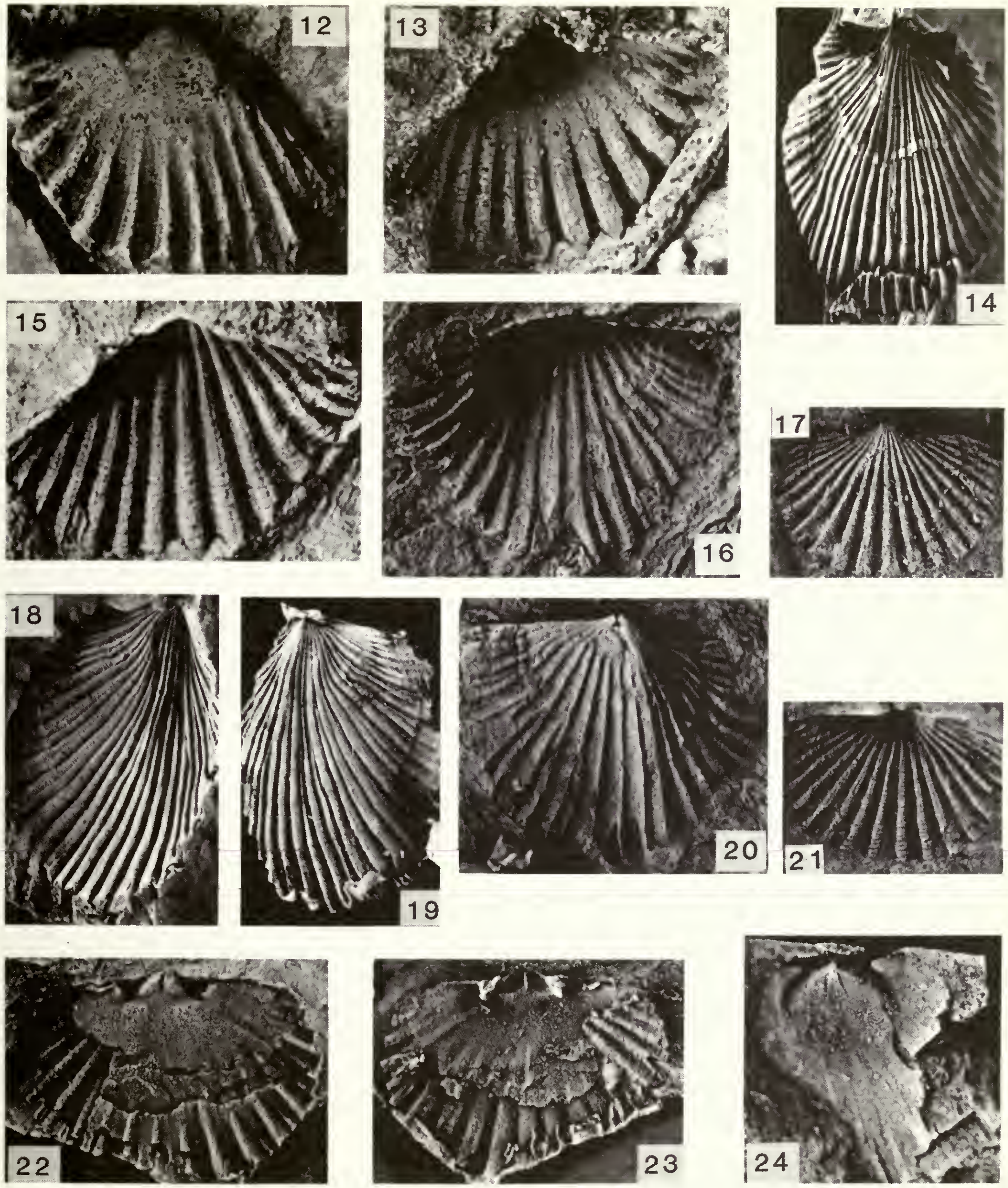




Figs 2–3 Craniid gen. et sp. indet. BC 9171, external mould and latex cast of pedicle (?) valve, both × 10. Clashford House Formation.

Figs 4–5 Orthid gen. et sp. indet. BC 9175, latex cast and external mould of pedicle valve, × 4. Clashford House Formation.

Figs 6–11 *Plaesiomys* cf. *multiplicata* Bancroft. Figs 6, 7, BC 9172, latex cast and external mould of pedicle valve, both ×5⅓. Figs 8, 10, 9, BC 9173, internal mould, latex cast and external mould, respectively, of pedicle valve, all ×2⅔. Fig. 11, BC 9174, part of anterior margin of pedicle valve with borings (see p. 290), ×4. Clashford House Formation. See also Figs 12–24.



Figs 12–24 *Plaesiomys* cf. *multiplicata* Bancroft. Figs 12, 13, 14, BC 9176, internal mould, latex cast and external mould, respectively, of pedicle valve, all × 12. Figs 14, 18, 19, BC 9177, external mould of pedicle valve and external mould and latex cast of brachial valve, all × 3. Figs 16, 20, BC 9178, external mould and latex cast of pedicle valve, both × 5. Figs 17, 21, BC 9179, latex cast and external mould of pedicle valve, both × 6. Figs 22, 23, BC 9180, internal mould and latex cast of brachial valve, × 5½. Fig. 24, BC 9181, internal mould of pedicle valve, × 5. Clashford House Formation. See also Figs 6–11.

costellae and interspaces; 16–20 costae are present on 1, 0, 3, 0 and 1 valve exteriors, at 5-mm growth stage 28–32 costae and costellae are present on 1, 0, 2, 0 and 1 valve exteriors, whilst two valves yield approximate counts of 40 and 46 ribs at the 10-mm growth stage; one valve exterior shows about 50 ribs at the 15-mm growth stage. Concentric ornament of fine growth lines.

Ventral interior with small, stout teeth directed dorsilaterally from anterior margins of delthyrium; they are supported by strong, receding dental plates which are inclined posterolaterally and fade anterolaterally, confining the muscle field. Subtriangular to subcordate ventral muscle scar about three-quarters as long as wide extending anteriorly to about three-eighths valve length. Compound scar comprises thin lanceolate adductors flanked by subtriangular diductor lobes, each about one-sixth valve width. Elsewhere external ornament strongly impressed.

Dorsal interior with simple, linear cardinal process, slightly thickened posteriorly, situated on well-defined, anchor-shaped notothyrial platform which extends anteriorly as low, broad ridge to about one-third valve length. Posterolaterally-directed brachiophores, blade-like and widely divergent, are supported by stout club-like bases which converge slightly towards median ridge. Pair of relatively deep triangular sockets, defined by hinge and posterolateral faces of brachiophores and their bases. Laterally subcircular, poorly-defined scars impressed. Musculature comprising pair of suboval, anteriorly divergent depressions flanking cardinal process and pair of less well-defined adductor scars situated anterolaterally to notothyrial platform.

Discussion. The Herbertstown specimens are most similar to those of *Plaesiomys multiplicata* Bancroft from the Soudleyan rocks of the Glyn Ceiriog area, north Berwyns (Bancroft 1945: 245; Cocks 1978: 50; Brenchley 1978: 150). This species is characterized by a transverse outline, fine ribbing, a flat notothyrial platform somewhat larger than the cardinal process and a well-defined marginal frill, usually most marked on the pedicle valve. The Irish species also has a transverse outline. Four pedicle valves have length to width ratios of 56, 58, 69 and 72% (mean: 64%) whilst the same statistic for six Welsh pedicle valves is 58, 59, 64, 71, 71 and 71% (mean: 66%). However, since the Herbertstown valves are commonly smaller than those from Glyn Ceiriog a direct comparison of these data is not warranted although both sets of statistics are clearly similar. The maximum width of both forms is located just anterior to the hinge line.

P. multiplicata is characterized by a fine costellate ornament. With 20–26 costae, however, it has slightly more than the Herbertstown valves, with 16–20, though certainly more data from both forms are required for a statistical assessment. Poor preservation and an insufficient sample size means we can say little about the ornamental development of the Irish species, except that pedicle valves have external costellae developed by the early growth stages in the manner of the Welsh form.

As far as can be judged the interiors of both forms appear similar. Although the ventral muscle scar on the best-preserved pedicle valve from the Clashford House Formation extends to 43% of the valve length and is 77% as long as wide, examination of topotype material of *P. multiplicata* demonstrates the size and shape of the ventral muscle scar to be fairly variable; the Irish specimens are similar to the studied topotype sample.

Bancroft (1945: 244) considered the presence of a marginal frill, particularly on the pedicle valve, to be diagnostic of both *P. robusta* Bancroft, 1945, and *P. multiplicata* and could serve to separate these Costonian and Soudleyan species from the finer-ribbed, post-Marshbrookian members of the genus. Although this feature is of doubtful taxonomic value there is evidence of such a frill on the larger valves (e.g. Fig. 11) of *P.* cf. *multiplicata.*

Cocks (1978: 50) has synonymized *P. multiplicata* with *Orthis flabellulum* J. de C. Sowerby *multifida* Salter, 1866, from rocks of Caradoc age, at Llyn Idwal, Snowdon. The Herbertstown specimens have been compared with the well-documented Glyn Ceiriog species on the basis of Bancroft's description and study of a topotype sample. Similarly Diggens & Romano (1968: 47) have assigned material, from the Soudleyan Multiplicata

Sandstone at Llyn Cowlyd, north Wales, to Bancroft's species. Comparison and assessment of Salter's species must await its detailed revision.

Subfamily **ENTELETACEA** Waagen, 1884

Family **DALMANELLIDAE** Schuchert, 1913

Genus ***OANDUPORELLA*** Hints, 1975

TYPE SPECIES. By original designation, *Oanduporella reticulata* Hints, 1975, from the Oandu Stage (Viruan Series) of the east Baltic.

Oanduporella cf. ***reticulata*** Hints 1975
Figs 25–37

cf. 1975 *Oanduporella reticulata* Hints: 19, 105; pl. 1, figs 1–15; pl. 2, figs 1–5.
1980*b* ?*Ravozetina*/*Onnizetina*; Mitchell *in* Romano: 206.

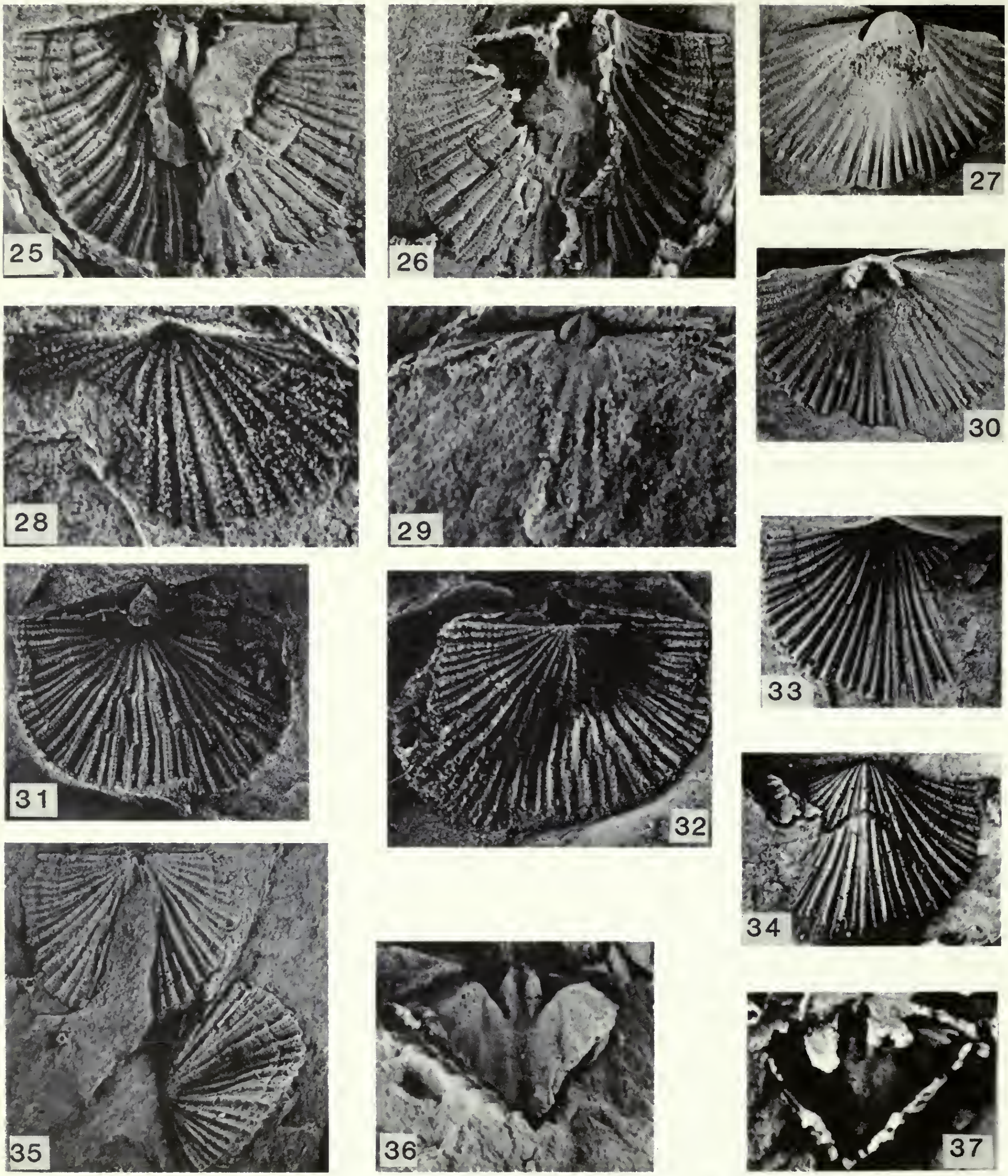
MATERIAL. Seventeen pedicle valves, eighteen brachial valves and four indeterminate valves. There are five conjoined pairs.

DESCRIPTION. Ventribiconvex valves of rounded transverse to subquadrate outline with maximum width just posterior to mid-valve length; hinge width about nine-tenths maximum width with angular and obtuse cardinal extremities. Pedicle valve about two-thirds as long as wide and about one-third as deep as long. Anterior profile convex with marked subcarinate axial surface and flatly convex flanks; lateral profile with maximum convexity at umbo, elsewhere valve surface weakly concave. Ventral interarea flat, with relatively wide, open delthyrium. Brachial valve about two-thirds as long as wide and about one-quarter as deep as long. Anterior profile with relatively deep and well-marked sulcus having flat, steeply inclined sides and an angular base, originating at about 1-mm growth stage and developing markedly anteriorly; flanks convex. Lateral profile with small convex umbo, elsewhere valve surface slopes gently anteriorly. Dorsal interarea short, flat and anacline; notothyrium open and wide. Radial ornament of strong costae and costellae of angular and subangular profiles with about 5–6 per 2 mm, medially at 5 mm growth stage; interspaces are rounded and semicircular, with net-like microsculpture of suboval pits with diameters of 0·1–0·15 mm at 4 mm medially from posterior margin.

Ventral interior with minute, subtriangular teeth supported by near vertical dental plates, which initially diverge anteriorly; at mid-length plates anteriorly convergent and confining muscle field. Muscle scars about as long as wide, extending anteriorly to about one-quarter valve length and comprising centrally situated adductors flanked by diductor lobes. Elsewhere external ornament weakly impressed.

Dorsal interior with cardinal process consisting of long linear shaft, expanded slightly posteriorly to form simple myophragm, and extending anteriorly to edge of notothyrial platform. Flanking brachiophores relatively thin and slightly divergent from their near-vertical, thicker, bases which extend ventrally from lateral margins of notothyrial platform. Platform about two-thirds as wide as long, extending to about one-quarter valve length, from where it continues anteriorly as low broad ridge, fading out near mid-valve length; high subparallel brachiophores and their bases flank crudely rectangular notothyrial chamber. Diductor scars impressed on floor of notothyrial platform which is bisected medially by cardinal process. Adductor scars relatively large, each elongately oval, about three-quarters as wide as long, and extending anteriorly from front of brachiophores and divided medially by low, broad ridge. Elsewhere external ornament feebly impressed, though locally microsculpture is well defined.

DISCUSSION. Hints defined her new genus *Oanduporella*, from the Oandu Stage of the Viruan Series in the east Baltic, in terms of its ventribiconvexity, elongate dorsal adductors



Figs 25–37 *Oanduporella* cf. *reticulata* Hints. Figs 25, 26, BC 9182, partly exfoliated dorsal interior and latex cast, both × 8. Figs 27, 30, BC 9183, internal mould and latex cast of pedicle valve, both × 5. Figs 28, 29, BC 9184, external and internal moulds of brachial valve, both × 14. Figs 31, 32, BC 9185, external mould and latex cast of brachial valve, both × 8. Figs 33, 34, BC 9186, external mould and latex cast of pedicle valve, both × 5. Fig. 35, BC 9187 (top) and BC 9188, pair of latex casts of external moulds of brachial valves, × 5. Figs 36, 37, BC 9189, internal mould and latex cast of brachial valve, both × 10. Clashford House Formation.

and fine, net-like microsculpture between the ribs (1975: 105). It is closely related to *Fascifera* Ulrich & Cooper, but differs in having stronger ribbing, more elongate dorsal adductor scars and in the intercostellate microsculpture. Wright (1981: 460) has discussed the significance of this microsculpture and considered the pits to represent the external appearance of caeca; the distinctive shell fabric results from the secretion of calcite at the mantle edge from cells surrounding puncta (Wright 1981: 460).

The Herbertstown material is assigned to *Oanduporella* and represents the first record of the genus from the British Isles; the microsculpture is particularly well developed on the shells of the smaller specimens, although on larger specimens the intercostal furrows are deeper and therefore the pitting is less obvious.

Although much of the Herbertstown material is deformed it appears comparable in shape and internal features to those of the type species, *Oanduporella reticulata* Hints (1975: 19, 105; pl. 1, figs 1–14; pl. 2, figs 1–5). The radial ornaments of both forms are similar; medially 5–6 costae and costellae are present per 2 mm at the 5-mm growth stage, and on brachial valve exteriors the following costellae are present by the 4-mm growth stage: $1a^{-}$, $2a^{-}$, $3a^{-}$, $4a^{-}$, $5a^{\circ}$, $5a^{-}$, $6a^{\circ}$, $6a^{-}$. The diameter of the pits on brachial valve exteriors of the Irish form is in the range 0·1–0·15 mm, medially at the 4-mm growth stage, which is similar to that noted for the Estonian species (see Wright 1981: 460).

Order **STROPHOMENIDA** Öpik, 1934

Suborder **STROPHOMENIDINA** Öpik, 1934

Superfamily **PLECTAMBONITACEA** Jones, 1928

Family **SOWERBYELLIDAE** Öpik, 1933

Subfamily **AEGIROMENINAE** Havlíček, 1961

Genus ***SERICOIDEA*** Lindström, 1953

Type species. By original designation, *Leptaena sericea* J. de C. Sowerby var. *restricta* Hadding, 1913, from the Chasmops beds (middle Ordovician) of the Fågelsång district, Sweden.

Sericoidea cf. ***abdita*** Williams 1955

Figs 38–42

cf. 1955 *Sericoidea abdita* Williams *in* Whittington & Williams: 418; pl. 39, figs 83–85.
aff. 1962 *Sericoidea* aff. *abdita* Williams; Williams: 188; pl. 18, figs 10–15.
cf. 1968 *Sericoidea abdita* Williams; Bates: 173; pl. 9, figs 3, 6.
cf. 1974 *Sericoidea* cf. *abdita* Williams; Williams: 139; pl. 24, figs 8, 9, 12, 15, 17, 18; pl. 28, fig. 16.
cf. 1978 *Sericoidea abdita* Williams; Cocks: 104.

Material. Six pedicle valves and two brachial valves, most of which are broken and poorly preserved.

Description. Minute, rectimarginate, planoconvex to concavoconvex valves of transverse to semicircular outline with maximum width at hinge line; cardinal extremities angular and acute. Pedicle valve with evenly convex anterior and lateral profiles, about two-thirds as long as wide and about one-fifth as deep as long. Brachial valve about two-thirds as long as wide with weakly concave anterior and lateral profiles. Ventral and dorsal interareas both short and flat – apsacline and anacline respectively; delthyrium apparently open, details of notothyrium not known. Radial ornament unequally parvicostellate with about 12 costae and costellae per mm, medially at and near the 2-mm growth stage. Fine concentric growth lines occasionally thickened to form feeble rugae. Ventral interior with small teeth marking anterolateral margins of delthyrium, not supported. Ventral muscle scar subcordate, comprising minute, elongately oval adductors surrounded by markedly larger diductor lobes; compound scar about as wide as long and extending anteriorly to about one-sixth valve length. Low broad ridge extends anteriorly from front of muscle scar to about three-fifths of valve length. Elsewhere external ornament strongly impressed and coarse pustules sporadically developed. Dorsal interior with prominent median septum flanked by at least three pairs of pustules; dorsal platform obscure. Cardinalia not known.

Discussion. The Herbertstown material is compared with *S. abdita* on account of its semicircular outline, ribbing density and apparently simple septule configuration in the brachial valve.

Family **LEPTAENIDAE** Hall & Clark, 1894

Genus ***KIAEROMENA*** Spjeldnæs, 1957

Type species. By original designation, *Leptaena kjerulfi* Holtedahl, 1916, from the Lower Chasmops Limestone (middle Ordovician) of the Oslo Region.

Kiaeromena sp.

Figs 43–46

Material. Two incomplete and relatively poorly preserved pedicle valves, slightly tectonically deformed.

Description. Large subquadrate pedicle valve with marked dorsal geniculation, about three-quarters as long as wide and about one-tenth as deep as long. Geniculation at approximately two-thirds valve length; disc about 20 mm long with curved trail about 15 mm long. Anterior and lateral profiles of disc weakly convex though modified locally by rugae; umbo prominent. Interarea short, flat and apsacline; delthyrium partly covered by small pseudodeltidium. Radial ornament of fine, unequal parvicostellae on both disc and trail numbering, medially, 5, 4 and 2 at the 5, 10 and 20-mm growth stages respectively. At least six fairly strong but variably developed concentric rugae restricted to disc with wavelengths of about 5 mm, having asymmetrical profiles with shorter, steeper posterior-facing slopes.

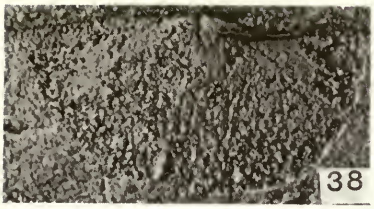
Ventral interior with small triangular teeth supported by widely divergent dental plates extending anteriorly to about one-tenth of valve length and confining the weakly impressed, elongately oval muscle scar. Valve interior pustulate.

Discussion. Although the only well-preserved valve of this species is tectonically deformed it is sufficiently distinctive and well enough preserved to allow an unequivocal generic placement. The Herbertstown material is most similar to *Kiaeromena* cf. *kjerulfi* (Holtedahl, 1916) from the Hagley Volcanic Group and Whittery Shales (both Soudleyan) of the Shelve inlier, and to *K.* cf. *kjerulfi* from the Allt Ddu Group (Soudleyan) of the Bala district. Further comparison with those forms and the Norwegian members of the genus (Spjeldnæs 1957) is not warranted on the available material.

Figs 38–42 *Sericoidea* cf. *abdita* Williams. Fig. 38, BC 9190, internal mould of pedicle valve, × 16. Fig. 39, BC 9191, internal mould of brachial valve, × 16. Fig. 40, BC 9192, internal mould of pedicle valve, × 12. Figs 41, 42, BC 9193, external mould and latex cast of pedicle valve, × 16. Clashford House Formation.

Figs 43–46 *Kiaeromena* sp.. Figs 43, 45, 44, 46, BC 9194, internal mould and latex cast of pedicle valve, and external mould and latex cast of same pedicle valve, all × 1½. (For borings, see p. 290). Clashford House Formation.

Figs 47–52 *Hibernodonta praeco* gen. et sp. nov. Figs 47, 50, BC 9195, latex cast and external mould of brachial valve, both × 6. Figs 48, 49, BC 9196, internal mould and latex cast of brachial valve, both × 6. Figs 51, 52, **Holotype** BC 9197, latex cast and internal mould of pedicle valve, both × 6. Clashford House Formation.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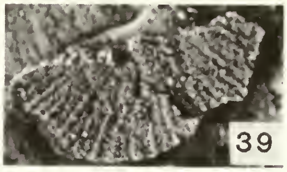
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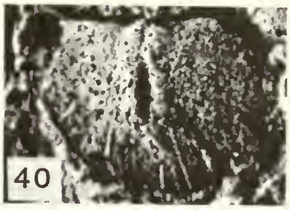
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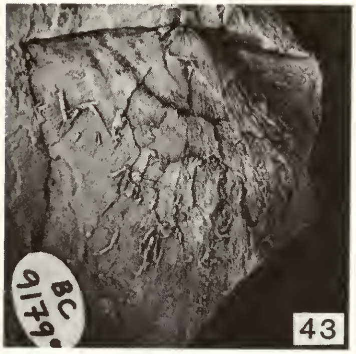

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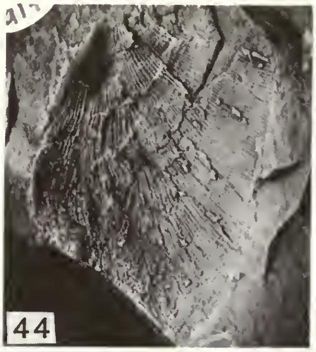
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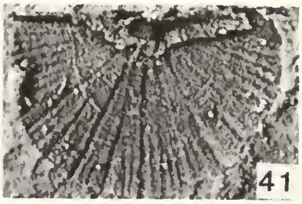
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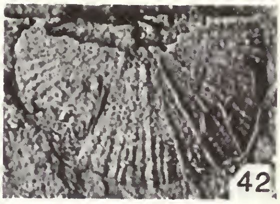
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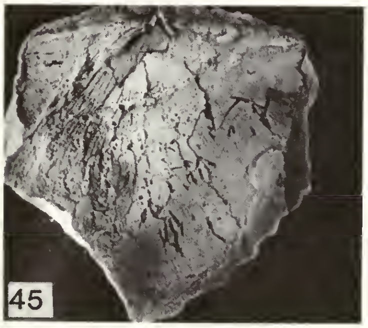
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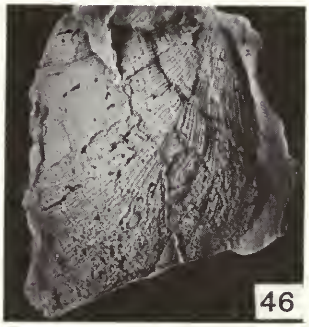
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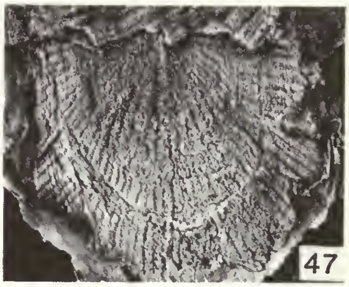
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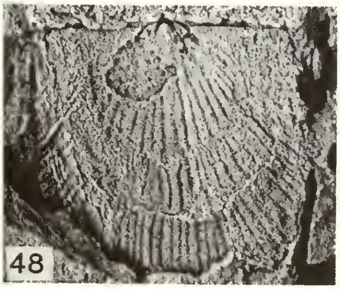
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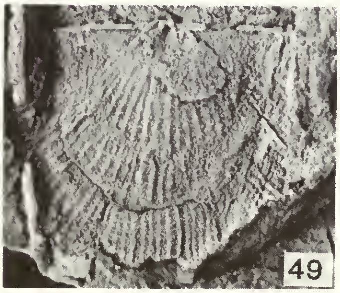
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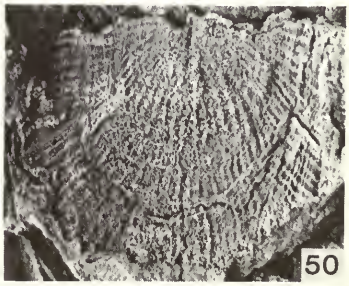
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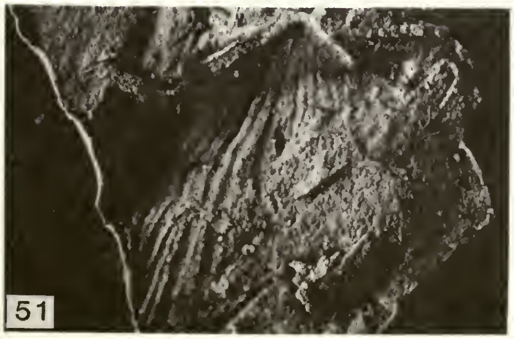
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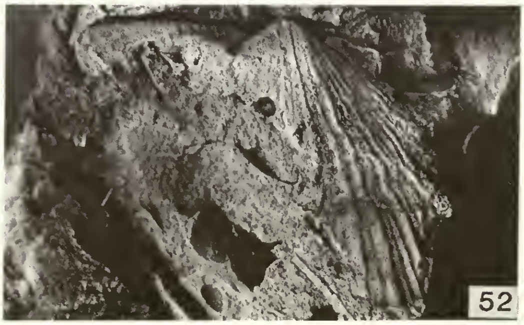
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Family **STROPHEODONTIDAE** Caster, 1939

Subfamily **STROPHEODONTINAE** Caster, 1939

Genus ***HIBERNODONTA*** nov.

NAME. Latin 'Hibernia' – Ireland.

TYPE SPECIES. *Hibernodonta praeco* gen. et sp. nov.; from the Clashford House Formation (middle Caradoc), near Herbertstown, Co. Meath, Ireland.

DIAGNOSIS. Small stropheodontinine genus with wide, open delthyrium, widely divergent dental plates and prominent arched chilidium. Ornament of dichotomously branching costae and costellae; the median costa commonly accentuated. Rugae variably developed.

DISCUSSION. The new genus possesses many of the features usually ascribed to *Rafinesquina* Hall & Clarke, 1892. In particular the outline and profiles of each valve, the cardinalia and ventral musculature are virtually identical. The presence of denticles along much of the hinge line, however, suggests the inclusion of the Herbertstown material within the Stropheodontidae.

Amsden (1974: 52–53) discussed the morphology of the type species of *Rafinesquina, Leptaena alternata* Conrad, from the Trenton Limestone, and assessed the generic features of the closely related *Eostropheodonta* Bancroft, 1949. He could not confidently discount the presence of denticles or striations on the teeth of one ventral interior of *L. alternata* examined, but emphasized that similar denticles are present on the teeth of many specimens assigned to *Rafinesquina* in the collections of the United States National Museum. Thus although *Brachyprion stropheodontoides*, a form he described from the Noix Limestone of Missouri, possesses many of the attributes of *Eostropheodonta*, for example the denticulate teeth and dental plates, an open delthyrium and a chilidium, Amsden (1974: 52–53) preferred to assign the species to *Rafinesquina* tentatively, pending a more complete revision of that genus. The fundamental difference between the two genera is generally accepted as the presence of denticles or striations on the teeth in *Eostropheodonta*; however it is noteworthy that Havlíček (1967: 81) considered such a difference insufficient to place that genus within the Stropheodontidae but preferred to have it in the eponymous family within the Strophomenacea. Havlíček considered that the Eostropheodontidae represent a distinct stock derived independently from the Rafinesquinidae, not intimately related to the stropheodontids (cf. Williams 1953). A number of other strophomenaceans have developed similar dental striations or denticles and have as a result been erroneously referred to, for example, *Eostropheodonta* (e.g. *Oepikina williamsi* (Spjeldnæs, 1957) from the middle Ordovician of the Oslo region) and *Stropheodonta* [*sic*] (e.g. *Strophomena bilix* (Lamont, 1935) from the Lower Drummuck Group (Cautleyan Stage – Ashgill Series) of the Girvan district). *Aphanomena* Bergström (1968: 13), however, has denticles developed on the socket ridges and is thought to have been derived from a *Kjaerina*-like form. Although the significance of these features within those stocks has yet to be assessed in detail, they serve to demonstrate that the development of this type of dentition is polyphyletic.

Cocks (1978: 124) commented upon stropheodontid classification; he considered that denticles probably arose in three lineages independently. The first group contains those forms which may have evolved from *Rafinesquina* and includes *Eostropheodonta*. Although this is almost certainly true, as discussed previously that genus is better retained outside the Stropheodontidae. *Hibernodonta*, however, is quite different and possesses many features typical of the more primitive, *Rafinesquina*-like stropheodontids. The delthyrium is wide and open whilst the notothyrium is closed by a large chilidium; dental plates are well developed and these diverge anteriorly. In the first two respects *Hibernodonta* resembles *Origostrophia* Mitchell, 1977 from the Killey Bridge Formation (Cautleyan Stage – Ashgill Series) of Pomeroy, Northern Ireland. However, the Herbertstown genus possesses well-developed dental plates; evidence of a pedicle foramen or ventral process is lacking. Although both genera have a thickened median rib the Pomeroy specimens have a much finer costellate ornament.

Excluding *Eostropheodonta* from the Stropheodontidae proper, the available evidence would indicate *Hibernodonta* as clearly one of the progenitors of the subsequent stropheodontinine plexus which flourished during the Silurian.

Hibernodonta praeco gen. et sp. nov.

Figs 47–52

Name. Latin '*praeco*' – a herald or crier.

Material. Two pedicle valves, three brachial valves and four indeterminate valves all relatively complete.

Holotype. A pedicle valve, BC 9197. British Museum (Natural History), London.

Diagnosis. A *Hibernodonta* species of elongate subquadrate outline with a radial ornament of dichotomously branching costae and costellae numbering about five per mm, medially, at the 5-mm growth stage; concentric growth lines variably thickened to form rugae.

Description. Relatively small, planoconvex valves of elongate subquadrate outline with maximum width at hinge line; cardinal extremities sharp and rectangular. Anterior commissure rectimarginate. Pedicle valve about as wide as long and about one-quarter as deep as long. Anterior profile gently convex with maximum curvature medially; lateral profile convex posteriorly to near mid-valve, flattening anteriorly. Interarea flat, about one-tenth of valve length and apsacline; wide, open delthyrium, the margins of which diverge anteriorly at right angles and are continuous with the dental plates. Hinge line denticulate along at least three-quarters of width. Denticles with rounded profiles, expanded slightly anteriorly, with outermost few directed anterolaterally; they number about 5 per mm and are situated on a low denticular plate which is about two-fifths as long as interarea. Brachial valve about four-fifths as long as wide with anterior and lateral profiles essentially flat, modified locally by strong concentric growth lines and rugae. Interarea flat, short and anacline, bearing complementary sockets and ridges. Notothyrium covered by prominent, arched chilidium. Ornament of evenly rounded costae and costellae which anteriorly develop markedly. About 20 arise at the umbo, the median six of which commonly branch dichotomously at or near the 2-mm growth stage; median rib thickened throughout early growth stages. Concentric ornament of fine concentric growth lines variably developed as rugae.

Ventral interior with pair of thin, virtually vertical, dental plates which diverge widely anteriorly from margins of delthyrium. Deep conical sockets present between dental plates and hinge. Muscle scars faintly impressed.

Dorsal interior characterized by a pair of strong cardinal process lobes which are markedly expanded posteroventrally, converging posteriorly and situated on low notothyrial platform with deep median depression. Socket ridges fairly short, slender, arising just lateral to posterior end of cardinal processes and diverging anteriorly at about 120°.

Discussion. For the present no other species can be assigned to *Hibernodonta* and little biometrical data are available to define the relative dimensions of the material and their variation.

Systematic palaeontology: Trilobita

Family **AULACOPLEURIDAE** Angelin, 1854

Subfamily **AULACOPLEURINAE** Angelin, 1854

Genus ***HARPIDELLA*** M'Coy, 1849

Type species. By monotypy, *Harpes megalops* M'Coy, 1846: 54–55; pl. 4, fig. 5; from the Upper Llandovery at Boocaun, Cong, Co. Galway.

Harpidella? sp.
Fig. 53

Material. An incomplete internal mould of a cranidium.

Discussion. This specimen broadly resembles several Ordovician species which historically have been ascribed to *Otarion* Zenker. As Owen & Bruton (1980: 19) noted, these forms should now be excluded from *Otarion* in the light of Thomas & Owens' work (1978), but their generic placement remains unclear. The absence of S2 in the Herbertstown cranidium suggests placement in *Cyphaspis* Burmeister, but the glabella does not overhang the preglabellar field and thus resembles *Harpidella*. A tentative ascription to the latter genus broadly follows the approach adopted by Owen & Bruton and others.

The small L1 in the present specimen invites comparison with '*Otarion*' sp. A of Tripp (1962) and '*O.*' sp. B of Tripp (1976) from, respectively, upper Llanvirn and lower Llandeilo strata near Girvan, south-west Scotland. Both these forms, however, have a longer (sag., exsag.) preglabellar field. In addition, '*O.*' sp. A has a very strongly tapered glabella and '*O.*' sp. B has a more elongate glabella. The *Harpidella* sp. cranidium figured by Tripp (1980: pl. 2, fig. 24) from the lower Ardwell group (middle Caradoc) near Girvan has a similar preglabellar field to that of the Herbertstown specimen but has a more elongate glabella and L1.

Family **ENCRINURIDAE** Angelin, 1854

Subfamily **CYBELINAE** Holliday, 1942

Genus ***DEACYBELE*** Whittington, 1965

Type species. Original designation, *Calymene arenosa* M'Coy, 1846: 47; pl. 4, fig. 12; from probable Caradoc strata at Ballygarvan Bridge, New Ross, Co. Wexford.

Discussion. *Deacybele* was diagnosed originally (Whittington 1965: 46–48) to comprise a group of Caradoc cybelines in which the glabellar lobes are large and discrete. Details of the anterior cranidial border were not known at that time. Owen & Bruton (1980) illustrated this area in *D. gracilis* (Nikolaisen, 1961) where it is developed as a single tubercle-like projection similar to that of *Cybeloides* Slocom. Owen (1981) described a lower Ashgill species, *D. conjuncta*, in which there is coalescence of the lateral parts of the glabellar lobes in some specimens. As Owen (1981: 55) noted, this may represent a reversion to the condition in *Cybeloides*, if that was the ancestor of *Deacybele*, or may indicate that *Deacybele* is not a monophyletic group but represents the repeated development of discrete lobes within *Cybeloides*. As an added complication, it should be noted that the 'compound lobes' (pulvini) in *Cybeloides* were shown by Evitt & Tripp (1977) to contain elements of the fixed cheeks incorporated in the glabella during ontogeny, and thus the discrete lobes in species of *Deacybele* may not be truly homologous with the glabellar lobes in other trilobites.

The Herbertstown cranidium has discrete lobes on the glabella and its overall morphology is close to that of the type species of *Deacybele, D. arenosa*. The anterior margin is preserved and, unlike *D. gracilis*, shows an arc of small tubercles in front of a shallow furrow and thus resembles the condition in *Atractopyge* and *Cybellela*. A cranidium of *D. conjuncta* illustrated by Owen (1981: pl. 12, fig. 24) shows a similar structure. Thus the variation between species currently assigned to *Deacybele* now throws considerable doubt on the phylogenetic homogeneity of the genus. This will only be resolved satisfactorily once more material of the less completely known species (including the type species) is available and other relationships within the Cybelinae as a whole have been clarified.

Deacybele aff. ***arenosa*** (M'Coy 1946)
Figs 54–59

Material. Three cranidia, two free cheeks, two hypostomata and a pygidium. Most specimens are internal moulds but counterpart external moulds of two cranidia and the pygidium are present.

Description. Despite the fragmentary condition of most of the specimens, a fairly full description can be given. Cranidium having a sagittal length equal to approximately 25% of the posterior width. Glabella concave-sided with the width of the occipital ring approximately equal to that of the frontal lobe. Occipital ring occupies approximately 20% of the sagittal glabellar length, tapering markedly distally and bearing a prominent median tubercle on its posterior half. Occipital furrow transversely directed. Three pairs of glabellar lobes occupy a little over 50% of the transverse glabellar width. L1 almost completely circumscribed by furrows. L2 transversely-directed, ridge-like, not quite as extensive abaxially as the other two lobes. L3 expanding a little abaxially. S3 diverging forwards at 130° although this figure may have been increased by distortion. Anteriorly the glabella is delimited by a very weakly impressed furrow which is arched strongly forwards. In front of this is a narrow (sag., exsag.) border bearing a single arc of small tubercles. Dorsal furrow deepest opposite L2. Posterior border narrow proximally, broadening (exsag.) considerably abaxially. Genal angle rounded. Posterior border furrow transversely-directed and deep over most of its length, but curving gently forwards and shallowing distally. Base of palpebral stalk situated opposite L2 and a weak eye ridge directed towards L3. Posterior branch of facial suture transversely-directed. Details of anterior branch not known. External and internal surfaces of glabella bear small scattered granules, and prominent paired tubercles are situated approximately between the ends of L1, S2 and S3 and on the mid-part of the frontal lobe. Field of fixed cheek bears a few granules set against a subdued, dense pitting.

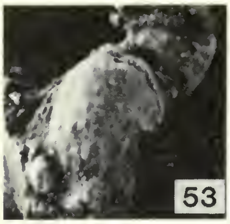
Border of free cheek weakly swollen, defined by a shallow border furrow. Internal mould of field bears a large number of irregularly distributed granules.

Hypostoma broadly similar to that of *Cybeloides* (*Paracybeloides*) (e.g. Ingham 1968: pl. 1, fig. 15) in having a swollen rhynchos (see Evitt & Tripp 1977: 114), swollen maculae and a triangular outline. This is the first hypostoma to be ascribed to *Deacybele* and emphasizes the similarity of many aspects of the genus to *Cybeloides*. The anterior margin is arched gently forwards, the lateral borders narrow and ridge-like and the posterior borders are broad, converging rearwards at about 80°.

Thorax not known. Length of pygidium (excluding spines) approximately equal to maximum width. Rachis tapers gently rearwards, occupying 70% of pygidial length and comprising a large articulating half-ring and at least 12 rings. Only the first ring is distinct over the entire width of the rachis; the others are only defined laterally. Four pairs of pleural ribs are present. The anterior rib has a well-developed anterior band. Those of the second and third ribs are less conspicuous and the posterior rib lacks such a band. First three pairs of pleural ribs arched abaxially. Fourth pair follows the sides of the posterior part of the rachis and converges at the same angle behind the rachis to the level at which, presumably, the ribs fan outwards as spines although this is not preserved in the only specimen available.

Discussion. The type species of *Deacybele, D. arenosa*, was redescribed by Whittington (1965: 48–49; pl. 14, figs 1–6; text-fig. 3A) on the basis of topotype cranidia from the probable Caradoc strata at Ballygarvan Bridge, Co. Wexford and a cranidium from Lower Caradoc strata at Greenville, Enniscorthy (see Brenchley *et al.* 1977: 70). This material is incomplete and details of the anterior margin of the cranidium are not clear. Nevertheless, the Herbertstown cranidia show several similarities to *D. arenosa*, most importantly in the absence of genal spines. The more transverse outline of the glabellar lobes in the present material is almost certainly a result of deformation which is also reflected in the development of transverse ridges crossing the glabellar stem. The main feature distinguishing this material from *D. arenosa* is the development of distinct paired tubercles on the glabella in the Herbertstown form.

D. pauca Whittington, 1965 from middle Caradoc strata in north Wales and *D. gracilis* (Nikolaisen, 1961) from upper Caradoc and lowest Ashgill horizons in Norway differ from *D. arenosa* and *D.* aff. *arenosa* in having genal spines. The anterior part of the cranidium in *D. pauca* is not known but that of *D. gracilis* is a single tubercle-like projection (Owen & Bruton 1980). *D. conjuncta* Owen, 1981 from the lower Ashgill of Norway appears to lack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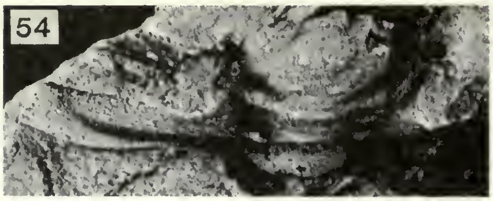
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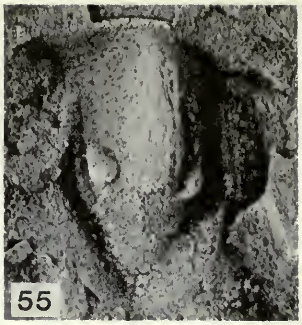
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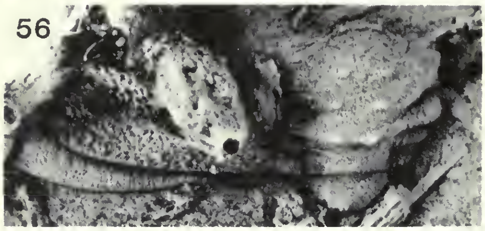
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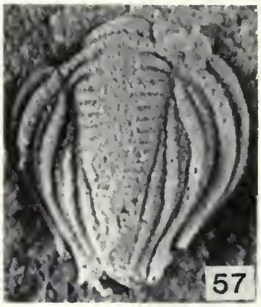
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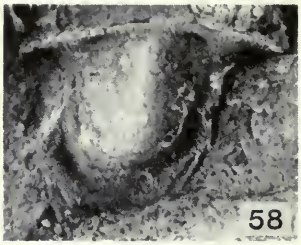
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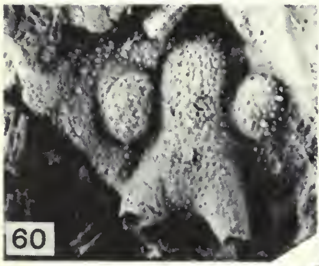
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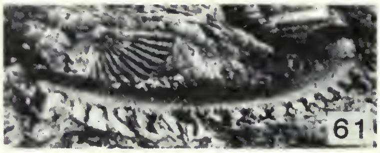
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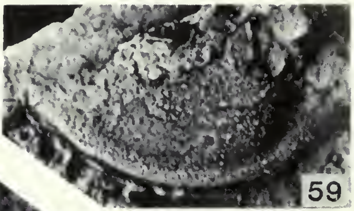
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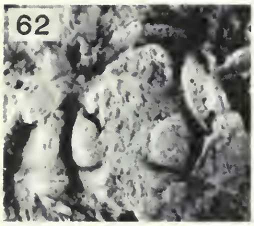
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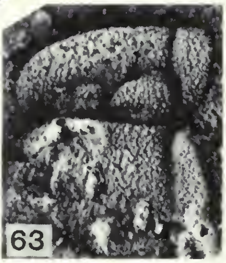
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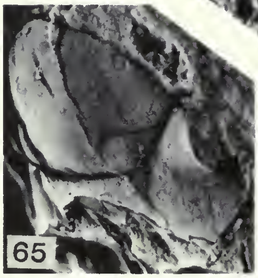
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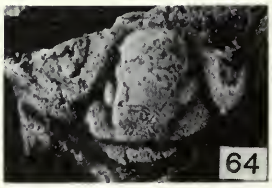
64

Fig. 53 *Harpidella*? sp. It 17040, dorsal view of incomplete internal mould of cranidium, × 7½. Clashford House Formation.

Figs 54–59 *Deacybele* aff. *arenosa* (M'Coy). Fig. 54, It 17042, dorsal view of cranidium, × 6. Fig. 55, It 17043, ventral view of latex cast of hypostoma, × 7½. Fig. 56, It 17042a, dorsal view of latex cast of cranidium (same specimen as Fig. 54), × 7. Fig. 57, It 17044a, dorsal view of latex cast of pygidium, × 14. Fig. 58, It 17041a, ventral view of latex cast of hypostoma, × 7½. Fig. 59, It 17045, lateral view of internal mould of free cheek, × 7. Clashford House Formation.

Figs 60–61 *Miraspis* sp. Fig. 60, It 17050, dorsal view of latex cast of cranidium, × 7½. Fig. 61, It 17051, lateral view of spinose lateral border of free cheek, ×7½. Clashford House Formation.

Figs 62–64 *Gravicalymene* sp. Fig. 62, It 17046, dorsal view of internal mould of distorted cranidium, × 7½. Fig. 63, It 17047a, lateral view of latex cast of cranidium, × 8. Fig. 64, It 17048, dorsal view of internal mould of cranidium, × 7½. Clashford House Formation.

Fig. 65 Lichid gen. et sp. indet. It 17049, ventral view of internal mould of distorted hypostoma, × 3. Clashford House Formation.

genal spines and has an anterior cranidial border like that of *D.* aff. *arenosa*, but differs in having a much denser glabellar granulation lacking paired tubercles and in some specimens having the glabellar lobes fused distally.

A single specimen of *D.* cf. *pauca* was recorded from the lower Caradoc Brickworks Quarry Shales of the Grangegeeth area further north (Romano 1980*a*). Although the specimen is incomplete, the genal angles and anterior border being missing, it differs from *D.* aff. *arenosa* in that the posterior borders are of more constant width (exsag.) and the occipital ring is less distinct.

Family **CALYMENIDAE** Milne Edwards, 1840

Subfamily **FLEXICALYMENINAE** Siveter, 1977

Genus ***GRAVICALYMENE*** Shirley, 1936

Type species. Original designation, *Gravicalymene convolva* Shirley, 1936: 409; pl. 29, figs 16–18; from the Birdshill Limestone (Ashgill), near Llandeilo, south Wales.

Gravicalymene sp.

Figs 62–64

Material. Four incomplete internal moulds of cranidia.

Discussion. The bell-shaped glabella and slightly sinuous dorsal furrows indicate that these cranidia belong in *Gravicalymene* (see Price 1982: 58 for a discussion of the genus). The preglabellar area is partially seen in one specimen (Fig. 62) where it is short (sag., exsag.) with a ridge-like, upturned anterior portion. This and the overall glabellar proportions suggests some affinity to *G. jugifera* Dean, 1962 (see also Ingham 1977) from Pusgillian strata in the north of England, but the present material is too poorly preserved for detailed comparison.

Family **LICHIDAE** Hawle & Corda, 1847

Lichid gen. et sp. indet.

Fig. 65

Material. One distorted hypostoma.

Discussion. This specimen is heavily distorted, the left side having undergone considerable shortening and the right side being expanded somewhat. The overall shape of the median body and the borders suggests an affinity to either *Platylichas* Gurich, 1901 or *Amphilichas* Raymond, 1905.

Family **ODONTOPLEURIDAE** Burmeister, 1843

Subfamily **MIRASPIDINAE** Richter & Richter, 1917

Genus ***MIRASPIS*** Richter & Richter, 1917

Type species. Original designation, *Odontopleura mira* Barrande, 1846: 57; from the Liten Formation (Wenlock) near Béroun, Czechoslovakia.

Miraspis sp.

Figs 60–61

Material. A free cheek (part and counterpart) and the external mould of an incomplete cranidium.

DISCUSSION. The stalked palpebral lobe and paired occipital spines indicate that this specimen belongs in *Miraspis*, although the latter feature alone is not diagnostic (Owen & Bruton 1980: 36). The combination of very robust occipital spines, large occipital ring, no median occipital protuberance, very weakly impressed occipital furrow and large extension of the fixed cheek behind L1 together distinguish the Herbertstown cranidium from other described species of *Miraspis*. The present specimen is too incomplete, however, to warrant the establishment of a new species at this stage.

The specimen is close to *M. solbergensis* Bruton, 1966 from the Boda Limestone (Ashgill) in Siljan, Sweden in terms of size of occipital ring, definition of occipital furrow and posterior fixed cheek development. The Swedish species, however, has a median occipital tubercle, more slender occipital spines, a less swollen median glabellar lobe, a more circular L1 outline and a much sparser cranidial granulation.

Miraspis sp. from the Brickwork's Quarry Shales of Grangegeeth (Romano 1980*a*) possesses less robust occipital spines, a more circular L1 outline and weaker furrows delimiting the median glabellar lobe than in the Herbertstown material.

Acknowledgements

We thank Dr L. R. M. Cocks and Mr R. P. Tripp for useful discussion and comments on the manuscript and Jenny Orr for her typing. D. A. T. Harper's contribution was carried out during tenure of NERC Research Award GR3/4471 and with travel funds fom the University of Dundee. W. I. Mitchell publishes with the permission of the Director of the British Geological Survey (NERC). The University of Dundee and BGS are thanked for further financial assistance during the preparation of this paper.

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Preliminary description of Lower Devonian Osteostraci from Podolia (Ukrainian S.S.R.)

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Synopsis

The osteostracans in the Zych collection of lower vertebrates from Podolia, belonging to the British Museum (Natural History), are described. There are 16 species which may be referred to either scolenaspidians or cephalaspidians, and a few undetermined osteostracans. One new genus and species, *Zychaspis siemiradzkii*, and two new species, *Stensiopelta pustulata* and *Mimetaspis glazewskii*, are described. Comments are added on Podolian species which have been very poorly diagnosed. The osteostracan fauna of Podolia is compared with that of the upper part of the Red Bay Group, Spitsbergen and Dittonian II of the Welsh Borderlands.

Introduction

Prior to World War II and particularly between 1934 and 1936, the Polish palaeontologist Wladislaw Zych collected excellent material of Lower Devonian osteostracans from the Podolian 'Old Red', with the help of Swedish and English sponsors. Consequently, part of this material was donated to the Naturhistoriska Riksmuseet, Stockholm, and part to the British Museum (Natural History). Zych began to publish this osteostracan material with the description of *Cephalaspis kozlowskii* (Zych 1937), in which he announced forthcoming monographs on the Osteostraci of Podolia. Unfortunately, this remarkable detailed anatomical description was the only paper he published on this subject, for his researches were interrupted by the war and a succession of tragic events which forced him to give up palaeontological activities.

Wladislaw Zych was born on 5 June 1899, in Bučač, a small village of Podolia (see map, Fig. 2, p. 313). After the liberation of Poland in 1920, he became Professor of Palaeontology at the Jana Kazimierza University of L'vov. During this period, he worked actively on the geology of the Devonian along the Dniestr valley and in adjacent areas (Zych 1927, 1931). When war broke out, Zych became a member of the resistance movements, fighting in Silesia and in the southeastern provinces of the Polish Republic. He was a commanding officer in the Z.W.Z., under the pseudonym 'Szary' ('the Grey'). In the middle of the war, he was arrested by the Germans and sent to two concentration camps, firstly Oswieçym (Auchwitz) and then Dachau. The severe maltreatment he underwent there injured his mind and he lost his memory, so was unable to restart his scientific activities after the war.

Zych then went to Italy, where he was given a position at the Osrodka Szkoleniowego, an organization providing scholarships for students whose studies had been interrupted by the war. With this organization, he came to England and decided to stay, devoting the rest of his life to catholic religious activities. He founded a chapel in St Briavel's, Glos., and worked actively for the 'Stettin' scout centre. He died on 22 May 1981, in Chepstow Hospital, and lies buried in the Hereford cemetery. For his activities during the war, Zych received both the Polonia Restituta Order and the golden cross of the Swedish Order of Wasa. His first steps in the field of lower vertebrate palaeontology were guided by the late Professor Erik Stensiö of Stockholm, who remembered him as a hard-working and humble person. His scientific work reflects his honesty by the care of the anatomical descriptions.

This paper is to report on the Podolian cephalaspid material represented in the collections of the British Museum (Natural History), and to compare it with the better-known

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osteostracan faunas of the Lower Devonian of Spitsbergen and Great Britain. It remains to be completed by future description of the specimens deposited in the Naturhistoriska Riksmuseet and in the Institute of Palaeontology of the Academy of Science, of the U.S.S.R. (Moscow) and of the Ukrainian S.S.R. (L'vov). Zych (1937) mentioned some specimens deposited in German institutions, but these are still elusive. Specimens belonging to the British Museum (Natural History) are referred to by register number with or without the prefix P; those belonging to other institutions are referred to with register number and with the full title of the institution.

Phylogeny and classification of the cornuate Osteostraci

The majority of the Osteostraci are represented by species which possess a pair of laterally pointed processes, the cornual processes, in front of the paired fins. These processes of the cephalic shield consist of endoskeletal and exoskeletal components and are likely to have appeared only once in the history of the group, yet they have been secondarily reduced or have even disappeared several times independently. The osteostracans with cornual processes have been referred to as 'cornuate' Osteostraci and are regarded as a monophyletic group (Janvier 1980, 1981*a, b*). This group probably arose from an ensemble of osteostracans which were primitively devoid of cornual processes, and are often referred to as 'non-cornuate' osteostracans (Ritchie 1967). Among the known non-cornuate osteostracans, some are more closely related to the cornuate ones than the others are, and thus this ensemble of primitive forms is paraphyletic (Janvier 1980, 1981*a, b*).

The interrelationships of the cornuate osteostracans are still obscure and consequently their systematics is mainly based on their degree of overall resemblance or divergence. This explains why, beside a small number of monophyletic groups with conspicuous autapomorphies, the majority of the cornuate osteostracans are represented by forms mainly with features ('horseshoe-shaped' shield) primitive for this group; these have in the past been referred to the genus *Cephalaspis*, because the type species of this genus, *C. lyelli* Agassiz, while one of the least known is apparently one of the least derived representatives of the cornuate Osteostraci. But it appears that the genus *Cephalaspis* has now to be restricted to its type species and perhaps a few others which share with it some synapomorphies, such as the shape of the median dorsal field or the elongate preorbital division of the shield. All the other known '*Cephalaspis*' species have to be referred to new genera, according to their respective phylogenetic relationships. In most cases, a careful revision of the specimens is needed before this can be achieved. Lankester (1870), Stensiö (1932, 1958), Denison (1951*a*), Wängsjö (1952) and Janvier (1980, 1981*a*) referred some of the species previously referred to as '*Cephalaspis*' to new genera, and this policy will be continued in the present paper, except when no particular phylogenetic position can be given to a '*Cephalaspis*'-like species.

I recognize five major monophyletic groups of still undetermined taxonomic rank among the cornuate Osteostraci: the cephalaspidians, kiaeraspidians, benneviaspidians, thyestidians and scolenaspidians (Janvier 1980, 1981*a, b*). All these groups are characterized by conspicuous autapomorphies, except perhaps for the cephalaspidians, the monophyly of which deserves to be more thoroughly tested. These five groups will be briefly commented on below. This classification of the Osteostraci will probably be modified in the future, following new investigations on the internal anatomy of the best-preserved non-cornuate forms (*Aceraspis, Hemicyclaspis*). At present, the lack of detailed information on the internal anatomy of the non-cornuate forms makes it difficult to use internal characters in determining the phylogeny of the cornuate forms, since out-group comparisons are impossible for these characters. For example, it is difficult to establish the significance of the presence or absence of the medial recess of the posteroventral myodome of the cornuate forms (Janvier 1980, 1981*a*).

The thyestidians are characterized by the medial course of the infraorbital sensory-line canal, which does not pass onto the lateral field, and by a relatively narrow pineal plate.

Most thyestidians, except the most primitive known species *Procephalaspis oeselensis* (Robertson), show two longitudinal rows of large tubercles on the dorsal face of the abdominal division of the shield. The thyestidians contain an important monophyletic subgroup, the Tremataspididae, characterized by the considerable elongation of the abdominal division and the loss of the paired fins (excluding *Tyriaspis, Didymaspis* and *Sclerodus*, which deserve a revision, but including *Timanaspis*). The sister-species of this highly derived subgroup is *Thyestes verrucosus* Eichwald, with which it shares the very narrow pineal plate, the enameloid cap on the tubercles (similar to the superficial layer of cosmine in tremataspids; Denison 1951*b*), the rows of large tubercles on the abdominal division, and the dermal denticles on the supra-oral field.

The kiaeraspidians are characterized by an elongate and narrow abdominal division which tends to become shorter in the most derived taxa, a considerable reduction of the cornual processes and of the prebranchial fossae, and an enlargement of the supra-oral fossae (Janvier 1981*a*).

The benneviaspidians have a dorsoventrally flattened shield. Their exoskeleton is generally devoid of ornamentation and lacks radiating canals in the middle layer.

The scolenaspidians have a massive and generally elevated shield characterized by a nasohypophysial opening in which the hypophysial division is larger (sometimes much larger) than the nasal division, and which opens in the floor of a relatively deep depression. The ornamentation of the scolenaspidian exoskeleton generally consists of large, rounded tubercles, and the scolenaspidians often possess a well-developed median crest or spinal process on the abdominal division. The cornual processes are generally thick, strongly curved medially, and ornamented with spiny tubercles.

Finally, the cephalaspidians may be defined by the condition of the first 'sinus expansion of the labyrinth' canal leading from the otic region to the lateral fields ('*s.e.l.*' canal), which branches at a point close to the orbit, bending there sharply. They also have lateral fields extending far backwards onto the dorsal face of the cornual processes. The latter are generally broad, flattened, but not very long. It must be stressed that the monophyly of this group is still uncertain.

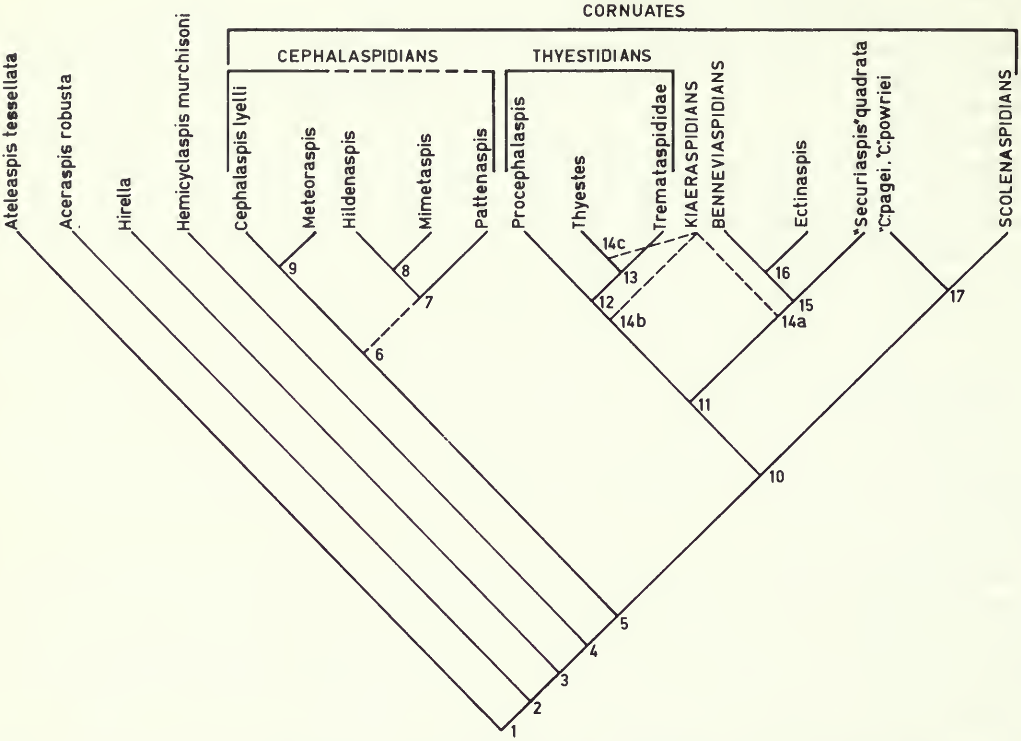
I include in the cephalaspidians the genus *Cephalaspis*, restricted to *C. lyelli* and a few other immediately related species, and the genus *Meteoraspis* (Janvier 1981*a*), characterized by lateral fields occupying only the lateral part of the cornual processes, and extending almost to the tip of the latter. The genera *Pattenaspis* (Stensiö 1958), *Mimetaspis* (Stensiö 1958) and *Hildenaspis* (Janvier 1976) are also provisionally placed in the cephalaspidians on the basis of the condition of the first '*s.e.l.*' canal.

The relationships between these five groups are still uncertain, mainly because of the difficulty of out-group comparisons with the non-cornuate forms. The cladogram proposed here (Fig. 1; Janvier 1981*a*) is admittedly supported by rather tenuous arguments and depends largely on a number of arbitrary generalizations, but it has not yet been refuted. There remains, for instance, an uncertainty as to the relationships of the kiaeraspidians, although I would be inclined to consider the structure of the posteroventral myodome (with no medial recess) shared by them and the thyestidians as a more reliable derived character than the 'orthobranchiate' condition, shared with the benneviaspidians.

The benneviaspidians, kiaeraspidians and thyestidians share at least one synapomorphy: the first '*s.e.l.*' canal branching at a point very close to the lateral field. I could find no satisfactory synapomorphy of the genus *Securiaspis* (Stensiö 1932), and I suspect that it may be paraphyletic, forming a possible stem-group for the three groups mentioned above.

The position given to the scolenaspidians in this cladogram is based only on the absence of a large median dorsal scute which replaces the anterior dorsal fin in *Hemicyclaspis* and the cephalaspidians. This lack of any trace of median dorsal scute is also known to occur in *Thyestes verrucosus* (and hence, perhaps, in all the thyestidians). The squamation of the trunk is unknown in the benneviaspidians and kiaeraspidians. By contrast, this large median scute, similiar to that of *Hemicyclaspis murchisoni* (Stensiö 1932) is known in *C. lyelli* (White 1958) and in *Meteoraspis pinnifera* (Wängsjö 1952). Although the lack of a character must be used with caution, it is, for the moment, the only available criterion for assigning the scolenaspidians to a particular position within the cornuate osteostracans. The ornamentation of the dermal skeleton of the scolenaspidians is more similar to that of the thyestidians and kiaeraspidians than to that of cephalaspidians and *H. murchisoni*, in which it is covered with a smooth cosmine-like hard tissue.

It would be premature to propose a Linnean classification of these major osteostracan groups, and I retain the admittedly imperfect classification outlined in this section, which does not suggest any particular taxonomic rank.


CORNUATES
CEPHALASPIDIANS
THYESTIDIANS
Ateleaspis tessellata
Aceraspis robusta
Hirella
Hemicyclaspis murchisoni
Cephalaspis lyelli
Meteoraspis
Hildenaspis
Mimetaspis
Pattenaspis
Procephalaspis
Thyestes
Tremataspididae
KIAERASPIDIANS
BENNEVIASPIDIANS
Ectinaspis
"Securiaspis" quadrata
"C." pagei, "C." powriei
SCOLENASPIDIANS
1
2
3
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14a
14b
14c
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16
17

Fig. 1 Theory of phylogenetic interrelationships of the Osteostraci (from Janvier 1980, 1981*a*). Key to the synapomorphies: *1*, cephalothoracic shield with median and lateral 'sensory' fields, horizontal lobe of the tail; *2*, solid marginal and rostral parts of the shield, slightly more stenobasal paired fins; *3*, stenobasal paired fins, large dermal plates on the ventral side of the shield; *4*, anterior median dorsal fin transformed into a large dermal scute, large trunk scales, cosmine-like dermal covering; *5*, cornual processes; *6*, first '*s.e.l.*' canal abruptly curved midway between the orbit and the lateral field, and branching at this point; *7*, slender cornual processes with medial denticles, ornamentation consisting of minute elongate tubercles; *8*, no independent pineal plate, large orbits; *9*, flattened cornual processes with lateral fields extending posteriorly onto them; *10*, no trace of anterior median dorsal fin, broad pectoral sinus (?), ornamentation consisting primitively of costulate tubercles (?); *11*, first '*s.e.l.*' canal branching near the lateral fields; *12*, infraorbital sensory-line canal running near the mid-line, narrow pineal plate; *13*, enameloid cap on the tip of the tubercles, elongate abdominal division bearing longitudinal rows of large tubercles, external opening of endolymphatic duct outside median dorsal field, small pineal plate, denticles on supra-oral field; *14a*, 'orthobranchiate' condition; *14b*, no medial recess of the posterior ventral myodome; *14c*, elongate abdominal division, short cornual processes; *15*, flattened shield, large pectoral sinus; *16*, strongly divergent cornual processes, very flat shield, broad posterior part of the lateral fields; *17*, hypophysial division of nasohypophysial opening slightly larger than the nasal division, and situated in a depression.

Geological setting

The geology of the Lower Devonian 'Old Red' of Podolia was first described by Zych (1927), who published the most reliable geographical data on the area where the osteostracan-bearing localities are located (Fig. 2). Later, Balabai (1962) published a simplified geological map of the area, showing the areal extent of the three major units defined by Zych. However, this map is largely erroneous. The Lower Devonian of Podolia has a monoclinal structure, dipping to the northwest, and crossed by the Dniestr valley which runs at right angles to the strike. Consequently, the oldest layers occur in the east (Borshchov) and the youngest in the west (Dniestr Series).

Three major horizons, or stages (cf. Nikiforova 1977, addendum), have been recognized in the Lower Devonian of Podolia: the Borshchov (Borszczow), Čortkov (Czortkow) and

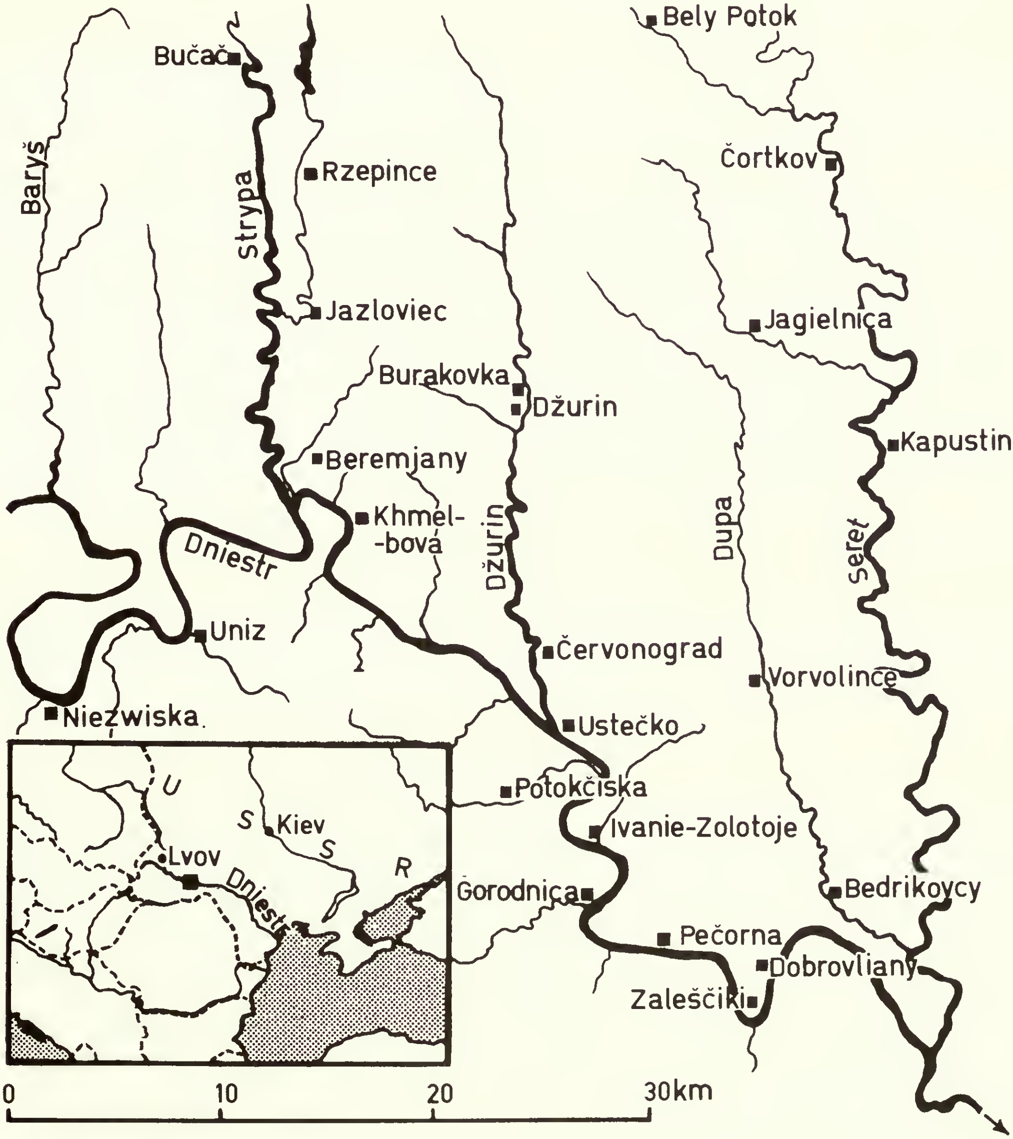
Bely Potok
Bučač
Baryš
Rzepince
Čortkov
Strypa
Jazloviec
Jagielnica
Burakovka
Džurin
Kapustincy
Beremjany
Khmel-
-bová
Džurin
Dupa
Seret
Dniestr
Uniz
Červonograd
Vorvolince
Niezwiska
Ustečko
U
S
Kiev
S
R
Potokčiska
Lvov
Ivanie-Zolotoje
Dniestr
Gorodnica
Bedrikovcy
Pečorna
Dobrovliany
Zaleščiki
0
10
20
30km

Fig. 2 Locality map. The locality names are transliterated from Ukrainian into the Latin alphabet. The Polish transliteration is indicated in the text.

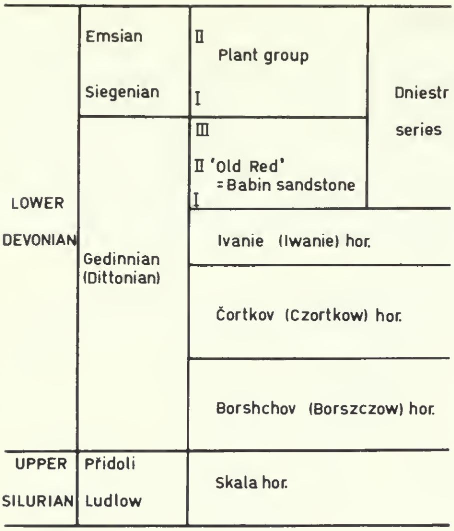

Fig. 3 Stratigraphy of the Lower Devonian and Upper Silurian of Podolia (from Zych 1927, Boucot & Pankiwskyj 1962, Balabai 1962 and Karatayute-Talimaa 1981).

Ivanie (Iwanie) horizons. The latter is overlain by the 'Old Red', or Babin Sandstone, which in its turn overlain by the Plant Group, referred to the Siegenian and Emsian. The 'Old Red' and Plant Group together form the Dniestr Series (Fig. 3).

The material described herein has been collected mainly in the 'Old Red' and Ivanie horizons, but the precise stratigraphical position of some finds is difficult to determine, because the labels written by Zych himself lack indication of the altitude at which they were found. Most of the exposures occur in the cliffs of the banks of the Dniestr and adjacent creeks. Some of these cliffs cut through several horizons and fossils coming from the same locality may belong to different faunal asemblages. Consequently, any precise stratigraphical conclusions arising from the present study can only be drawn by geologists who have access to the localities, and can compare the facies of the matrix of the specimens with those of the sections themselves.

Systematic descriptions

Most of the available Podolian osteostracans belong to the scolenaspidians, and only a few specimens can be referred to the cephalaspidians and, questionably, benneviaspidians. No kiaeraspidian or thyestidian has yet been recorded from the Lower Devonian of Podolia.

SCOLENASPIDIANS

The genus *Scolenaspis* was erected by Jarvik (1954) for *Cephalaspis signata* Wängsjö (1952), which shares with *C. lyelli* only primitive cornuate osteostracan characters. As early as 1870, Lankester had noticed that some of the '*Cephalaspis*' species of Great Britain were quite different from *C. lyelli* in the shape and ornamentation of the shield, and he proposed the subgeneric name *Zenaspis* for *C. salweyi* Egerton. The name 'zenaspidians' would thus have been more suitable for the monophyletic group called here scolenaspidians, but I prefer to keep the generic name *Zenaspis* for a restricted subgroup of the scolenaspidians, which is relatively derived by comparison with *S. signata*. The latter corresponds to a more generalized pattern of the group and the name scolenaspidian is thus more appropriate to designate the whole group.

The scolenaspidians comprise several groups of much derived forms, such as *Diademaspis, Zenaspis, Machairaspis*, and probably also *Tegaspis* (Fig. 4), and an ensemble of less derived forms which have a shield of '*Cephalaspis*' type (generalized cornuate osteostracan pattern),

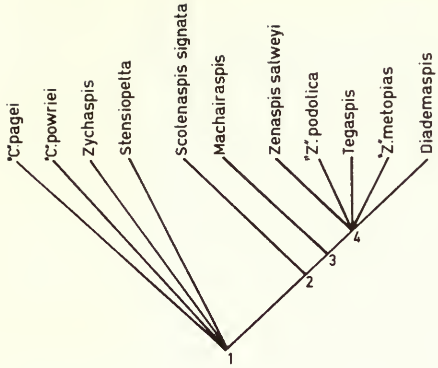

Fig. 4 Theory of phylogenetic relationships of the scolenaspidians and some closely related cornuate osteostracans. Key to the synapomorphies: *1*, hypophysial division of the nasohypophysial opening slightly larger than the nasal division, narrow and thick cornual processes, lateral fields with irregular limits; *2*, spinal process or prominent median dorsal ridge; *3*, hypophysial division of the nasohypophysial opening much larger than the nasal division, and situated in a deep depression; *4*, broad and massive shield, short cornual processes, coarse ornamentation, broad median dorsal field, posterior part of the lateral fields produced medially into a distinct lobe.

although showing the typical scolenaspidian characters. *S. signata* belongs to these 'stem' scolenaspidians and, for the moment, is the only species included in *Scolenaspis*. The species '*Cephalaspis*' *pagei*, '*C.*' *powriei* and '*C.*' *spinifer* (Lankester 1870, Stensiö 1932), from the Devonian of Great Britain, can also be regarded either as primitive scolenaspidians or as the closest relatives of that group. They show incipient scolenaspidian characters (shape of the nasohypophysial opening, ornamentation, outline of the lateral fields) and any one of these three species may be regarded as the sister-species of all scolenaspidians. A theory of interrelationships of the scolenaspidians is presented in Fig. 4.

In the material from Podolia, as well as in that from Spitsbergen, highly derived and primitive scolenaspidians may coexist in the same locality. In Spitsbergen, however, the topmost part of the Wood Bay Formation (Stjørdalen Division) contains only remains of very large *Diademaspis* species. Some of the Podolian forms are quite similar to species known from Spitsbergen and Great Britain, but there are a few taxa which are unique to Podolia. The species which show only general scolenaspidian characters will be referred to here as '*Scolenaspis*'.

Genus *ZYCHASPIS* nov.

Diagnosis. Primitive scolenaspidians with a slight rostral lobe and slender cornual processes. The ornamentation of the exoskeleton consists of small, closely-set tubercles, and scattered large ones. The lateral fields are relatively narrow.

Name. After the late Dr W. Zych.

Type species. *Zychaspis siemiradzkii* sp. nov.

Remarks. The shield referred here to *Zychaspis* recalls in many respects that of some other primitive scolenaspidians or taxa closely related to them ('*C.*' *powriei* '*C.*' *pagei*, '*C.*' *watsoni*), in particular in the shape of the median dorsal field, the type of ornamentation, and the shape of the cornual processes. The scolenaspidian characters are feebly expressed in *Zychaspis*, but the hypophysial division of the nasohypophysial opening is slightly larger than the nasal division. The shape of the lateral fields is also very much of scolenaspidian type, with irregular medial margin and slightly enlarged anterior ends.

The phylogenetic position of *Zychaspis* within the scolenaspidians cannot be determined. It is probably a primitive taxon in this group, but it is uncertain whether it shares unique characters with any of the known monophyletic subgroups of the scolenaspidians. *Zychaspis* resembles '*C.*' *campbelltonensis* (Whiteaves 1881, Robertson 1936, Pageau 1969), from the Devonian of Canada, in the shape of the rostral region of the shield and the cornual processes. However, I doubt that this resemblance can be regarded as an indication of close relationships. In point of fact, neither the ornamentation nor the shape of the nasohypophysial opening of this Canadian species is suggestive of scolenaspidian affinities (personal observations on various specimens from Campbellton, especially BM(NH) P.56167). I would thus be inclined to consider this resemblance a convergence.

Zychaspis siemiradzkii sp. nov.
Figs 5, 6

Diagnosis. A moderately large species of *Zychaspis* with medially curved cornual processes.

Holotype. BM(NH) P.17714, labelled by Zych as '*Cephalaspis siemiradzkii* var. *elegans*'; 'Old Red' (probably Ivanie horizon), Chomiakówka East, north of Bely Potok, Podolia (now Ukrainian S.S.R.). Fig. 6.

Name. After Professor J. Siemiradzki, of the Geological and Palaeontological Museum, L'vov.

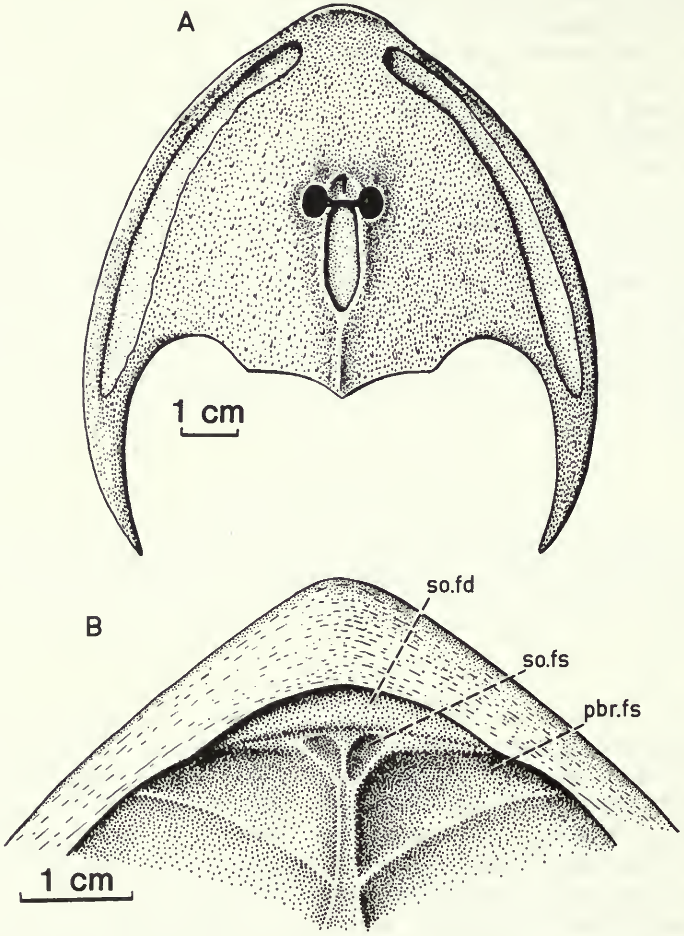

Fig. 5 *Zychaspis siemiradzkii* gen. et sp. nov., 'Old Red' and Ivanie horizons, Lower Devonian of Podolia, Ukrainian S.S.R. A, reconstruction of the shield, based on the holotype (P.17714) and numerous other specimens from the type locality, dorsal view. B, anterior part of the oralobranchial chamber, based on C.1324a in the Naturhistoriska Riksmuseet (Stockholm), ventral view. Abbreviations: pbr.fs, prebranchial fossa; so.fd, supraoral field; so.fs, supraoral fossa.

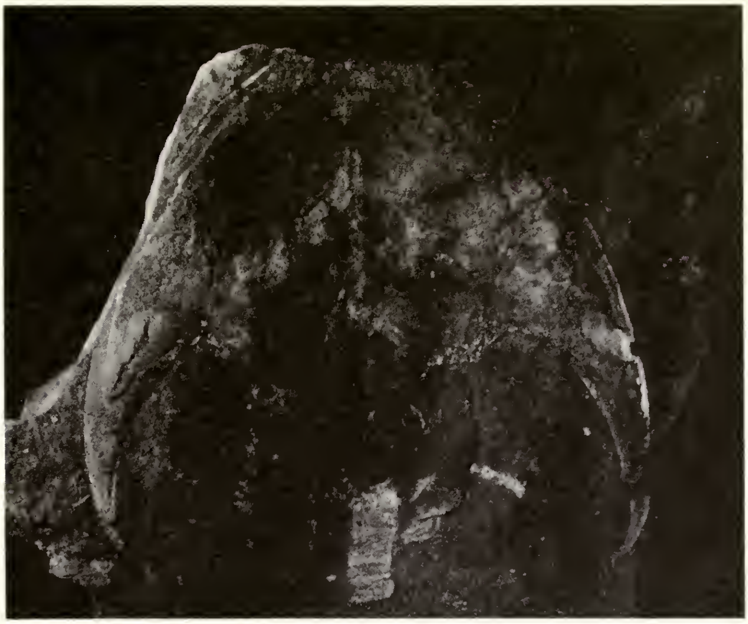

Fig. 6 *Zychaspis siemiradzkii* gen. et sp. nov., 'Old Red' (probably Ivanie horizon), Chomiakówka East, north of Bely Potok, Podolia, Ukrainian S.S.R. **Holotype** (P.17714), dorsal view. × 0·75.

MATERIAL. Holotype; Červonograd (Czerwonogrod): P.17717; Gorodnica (Horodnica): P.20457, P.20459, P.20461, P.20465, P.20470, P.20475–9, P.20480–2, P.20486–7, P.20492, P.20496, P.20504, P.20516–7, P.20548, P.53358–60, P.53363–8. All BM(NH).

REMARKS. This species is extremely abundant in the red-green sandstone of Gorodnica (or Horodnica on Zych's labels), which represents either the base of the 'Old Red' or the top of the Ivanie horizon.

Most of the specimens from Gorodnica are poorly preserved and much flattened. Many shields are only represented by the marginal and rostral rims and the cornual processes. The reconstruction in Fig. 5 is based on several specimens, including the holotype, Fig. 6. The rostral region is generally well defined and separated from the marginal region by a slight embayment, but in many specimens the rostromarginal transition is straight (Fig. 5B). The anterior part of the oralobranchial cavity can be observed in one specimen (C.1324a) in the Naturhistoriska Riksmuseet, Stockholm (Fig. 5B), and shows well-defined supraoral fossae (*so.fs*) and relatively large prebranchial fossae (*pbr.fs*). The pattern of fossae and ridges of this part of the oralobranchial cavity is like that in typical scolenaspidians, such as *S. signata* (Wängsjö 1952, Jarvik 1954). The median dorsal field is narrow and limited anteriorly by a thin, but separate, pineal plate. The ornamentation consists of very small closely-set tubercles. These are somewhat elongate in shape on the abdominal division, where one can also observe some scattered larger tubercles. This type of ornamentation resembles that of '*C.*' *powriei* from the Lower Devonian of Great Britain, but is probably a primitive type for scolenaspidians. The cornual processes are relatively slender, falciform and flattened. The lateral fields extend onto their proximal part only.

The two following species are referred with some doubt to the genus *Zychaspis*, since they have been erected by Balabai (1962) without adequate figures, and without reference to type specimens. I refer these species to *Zychaspis* on account of Balabai's sketches, which are reproduced as Fig. 7.

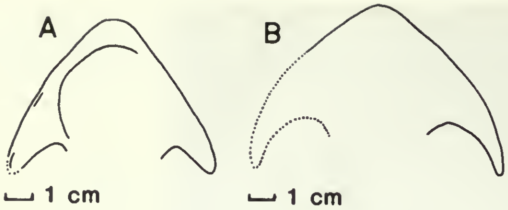

Fig. 7 *Zychaspis elegans* (Balabai), 'Old Red', Chmelbova, Podolia, Ukrainian S.S.R. B, *Zychaspis djurinensis* (Balabai), 'Old Red', Džurin, Podolia, Ukrainian S.S.R. (both after Balabai, 1962).

Zychaspis elegans (Balabai)
Fig. 7A

1962 *Cephalaspis elegans* Zych *in* coll.; Balabai: 7; fig. 10.

Balabai gave no diagnosis of this species, but the figure he published shows an elongate rostral region, as in *Z. siemiradzkii*, which is regarded as characteristic for the genus. In *Z. elegans* the cornual processes are more divergent than in *Z. siemiradzkii*. Type locality: Khmelbova, Podolia.

? *Zychaspis djurinensis* (Balabai)
Fig. 7B

1962 *Cephalaspis djurinensis* Balabai: 6; fig. 7.

This species did not receive any diagnosis in Balabai's paper. From the figure, it seems that the rostral region is produced anteriorly into a lobe as in *Z. siemiradzkii*, but the shape of the cornual processes is different, being stouter and more divergent. Type locality: Djurin, Podolia.

Genus *STENSIOPELTA* Denison 1951a

Diagnosis. Primitive scolenaspidians with very elongate, straight and strongly divergent cornual processes. Abdominal division elongate and narrow, with a slight median elevation just behind the median dorsal field. Short prehypophysial division of the shield.

Type species. *Cephalaspis woodwardi* Stensiö (1932); Abergavenny, Monmouthshire.

Remarks. The genus *Stensiopelta* was erected by Denison (1951*a*: 191) for *Cephalaspis woodwardi* Stensiö, which he regarded as very different from the other *Cephalaspis* species. Contrary to Wängsjö's footnote (1952: 250), this generic name is valid. Wängsjö (1952) considered *S. woodwardi* to be close to *Pattenaspis* ['*Cephalaspis*'] *deltoides* (Wängsjö) from Spitsbergen, but the resemblance in the shape of the cornual processes is superficial. *P. deltoides* belongs to the monophyletic genus *Pattenaspis*, characterized by the enlargement of the orbits, reduction of the prebranchial fossae (but in a way different from kiaeraspidians) and the elongation of the cornual processes. *Pattenaspis* does not share any synapomorphy with the scolenaspidians, whereas the two known species of *Stensiopelta* share with the scolenaspidians the shape of the nasohypophysial opening and the type of ornamentation, which consists of clusters of small rounded tubercles.

Stensiopelta pustulata sp. nov.
Figs. 8, 9, 10, 11

Diagnosis. *Stensiopelta* species with elongate abdominal division, and with an obtuse, slightly lobate rostral margin.

Holotype. BM(NH) P.17703–4, labelled by Zych as '*Cephalaspis woodwardi* var. *junior*'. 'Old Red' I, Ustečko (Uscieszko) West, Podolia, Ukrainian S.S.R.

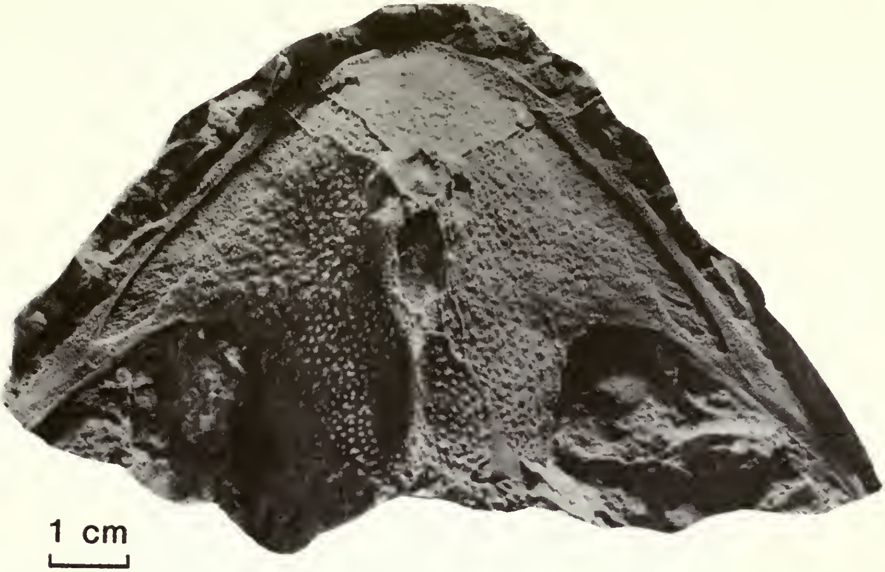

Fig. 8 *Stensiopelta pustulata* sp. nov., 'Old Red' I, Ustečko, Podolia, Ukrainian S.S.R. **Holotype** (P.17703), dorsal view. Silicone rubber cast from natural mould, whitened with magnesium oxide.

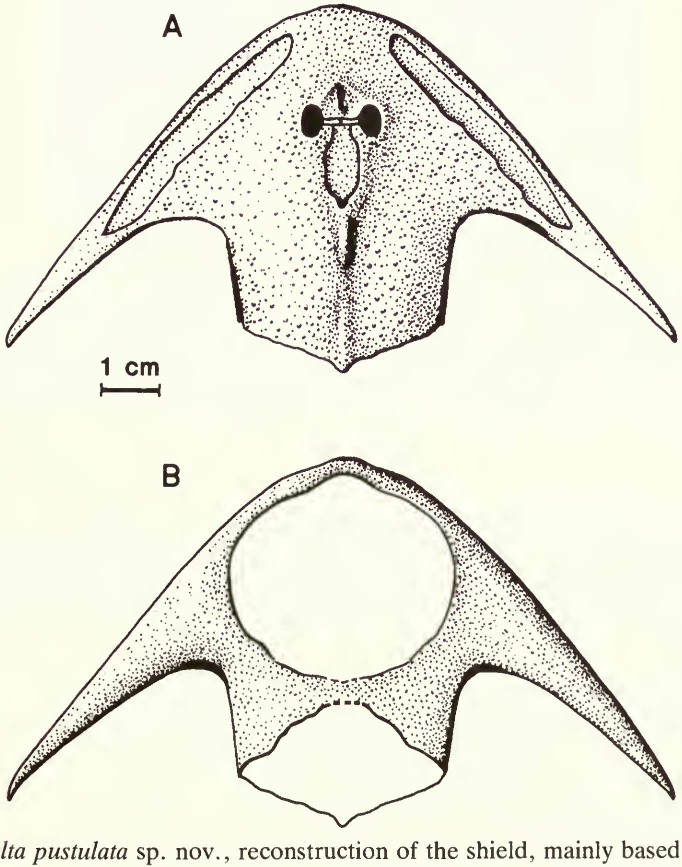

Fig. 9 *Stensiopelta pustulata* sp. nov., reconstruction of the shield, mainly based on the holotype (P.17703). A, dorsal view; B, ventral view.

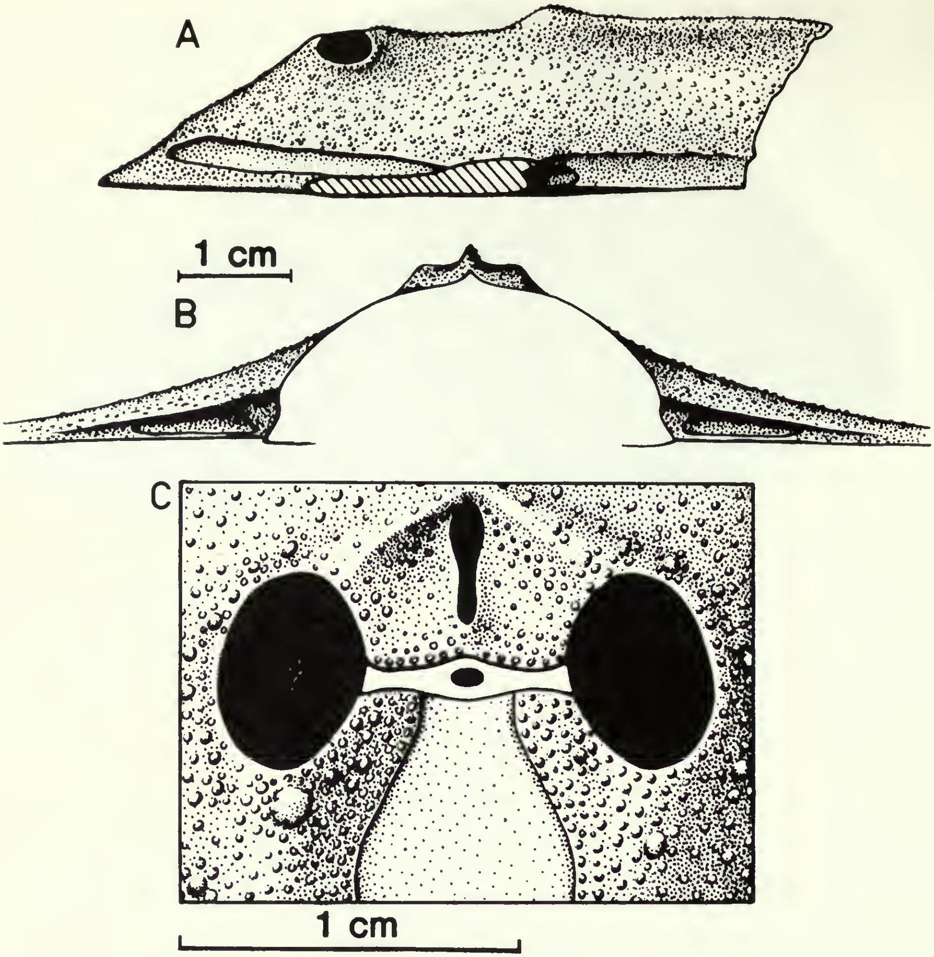

Fig. 10 *Stensiopelta pustulata* sp. nov., reconstruction of the shield, mainly based on the holotype (P.17703–4). A, lateral view; B, posterior view; the abdominal division has been cut just behind the area of attachment of the paired fins. C, orbital and nasohypophysial regions of the shield; the pineal plate is not known, and it is reconstructed here according to the shape of the groove which housed it.

NAME. From the pustulated type of ornamentation.

MATERIAL. (Well preserved specimens only). Holotype; Ustečko (Uscieszko): P.20534, P.20540–1; Burakóvka (Burakowka): P.17702; Bely Potok (Potok Bialy): P.17707; Červonograd (Czerwonogrod): P.20933; Gorodnica (Horodnica): P.20530–1, P.20553–4, P.20564–5. All BM(NH).

REMARKS. This species is slightly larger than *S. woodwardi* from the Lower Devonian of Wales (Stensiö 1932: fig. 51; pl. 20, figs 1, 2), and has a somewhat longer abdominal division. It differs also in having a more obtusely rounded rostral margin, which shows a faint rostral lobe, and in that the cornual processes of *S. woodwardi* are slightly less divergent than those of *S. pustulata*. Nevertheless, the two species can be regarded as extremely closely related.

The most noteworthy features of *S. pustulata* are the slight rostral lobe and the position of the median dorsal elevation of the abdominal division, which seems to be slightly closer to

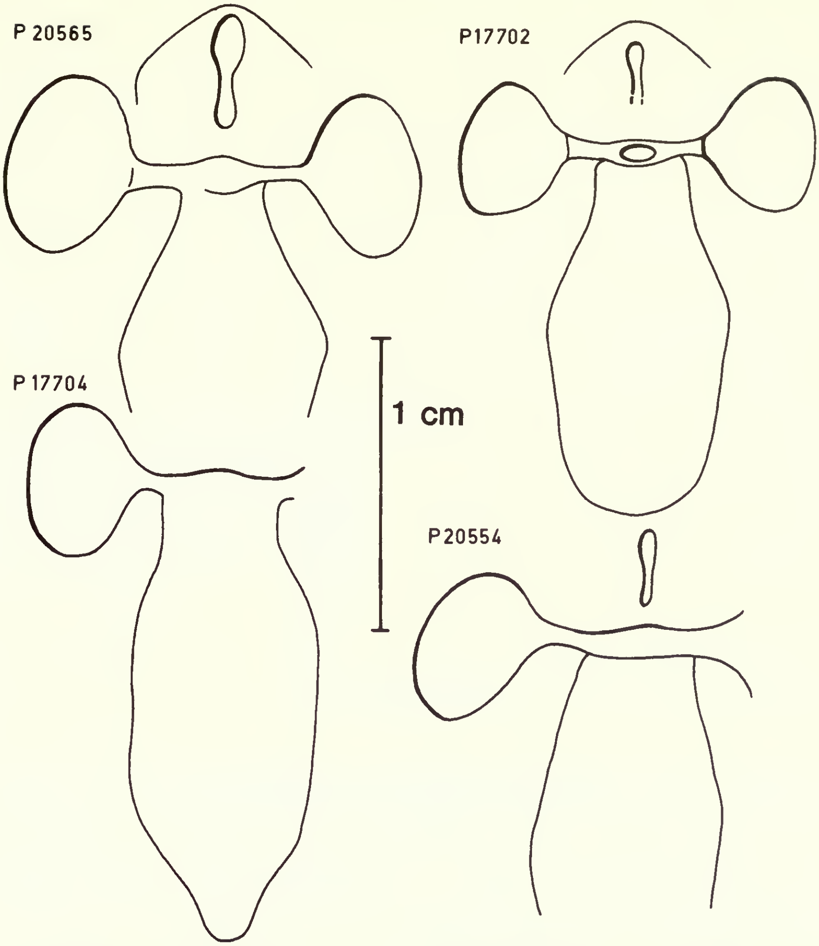

Fig. 11 *Stensiopelta pustulata* sp. nov.; variations in the shape of the median dorsal field.

the median dorsal field than in *S. woodwardi* (Figs 9A, 10A). As in *S. woodwardi*, the lateral flanges of the abdominal division are slightly concave behind the areas of attachment of the paired fins (Figs 9A, 10A, 10B). This longitudinal depression probably accommodated the medial edge of the fin.

The hypophysial division of the nasohypophysial opening is slightly enlarged (Fig. 10C), but this scolenaspidian character is not as well marked as in *Zenaspis* or *Diademaspis*. It is comparable to the condition in *Zychaspis* or '*C.*' *powriei*.

The ornamentation of the dermal skeleton consists of large tubercles, each surrounded by a ring of smaller ones. The large tubercles are generally in the centres of the tesserae. Between these patches of tubercles, the whole surface of the shield is covered with minute, scattered tubercles. The large tubercles are lacking on the cornual processes, the marginal region, the rostral region and the ventral side. This type of ornamentation is quite typical for scolenaspidians, and more closely resembles that of *Zenaspis* and *Diademaspis* than that of *Machairaspis* and the primitive forms of the group.

In all the other features of the shield (shape of the lateral and median fields, the orbits and the pineal plate), *S. pustulata* is very similar to *S. woodwardi*. There is, however, an important variation in the shape of the median dorsal field (Fig. 11), which may be more constricted anteriorly in some specimens than in others.

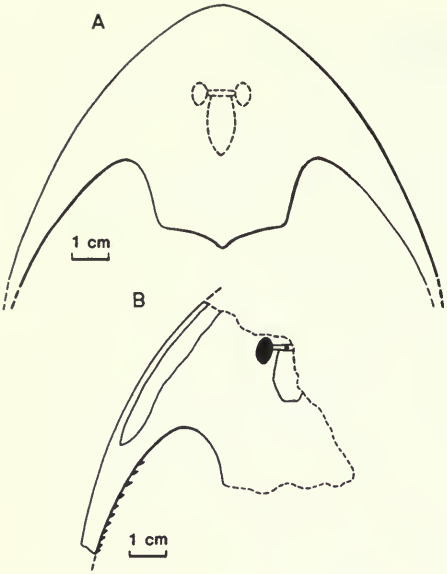

Fig. 12 *Stensiopelta* sp., labelled by Zych as '*Cephalaspis woodwardi* var. *subrotunda*'. A, P.17701, 'Old Red', Zascinovče (near Trembovla, on the Seret river), Podolia, Ukrainian S.S.R. B, P.17708, 'Old Red', Rcepinče, Podolia, Ukrainian S.S.R.

Stensiopelta sp.
Fig. 12

Some specimens have been labelled by Zych as '*Cephalaspis woodwardi* var. *subrotunda*', in particular P.17700–1 from Zascinovče ('Old Red') and P.17708 from Rzepiriče. This form differs from *S. pustulata* in its gently curved cornual processes. In P.17708 (Fig. 12B), the cornual processes bear medial denticles. These specimens may fall within the range of variation of *S. pustulata* or may belong to a different species. The material available, however, is not sufficient to determine this.

Genus *ZENASPIS* Lankester 1870

DIAGNOSIS. Medium-sized to large scolenaspidians with a broad median dorsal field and a very broad posterior part of the lateral field. Hypophysial division of nasohypophysial opening much larger than the nasal division. Low but sharp median dorsal crest (or spinal process) on abdominal division. Orbits comparatively small.

TYPE SPECIES. *Cephalaspis salweyi* Egerton (1857); Ludlow, Shropshire.

REMARKS. The name *Zenaspis* was erected by Lankester (1870: 43) as a subgenus of *Cephalaspis* for *C. salweyi*, which differs in many respects from *C. lyelli* (more massive shield, thicker cornual process, spinal process, tuberculate ornamentation). *Zenaspis* may be retained as a generic name for all the scolenaspidian species sharing the overall morphology of *Z. salweyi*, but there is no clear derived character for this genus, and the diagnosis given above contains characters which are possibly plesiomorphous for more derived scolenaspidian genera, e.g. *Tegaspis* and *Diademaspis* (Wängsjö 1952, Janvier 1980). We cannot therefore rule out the possibility that the genus *Zenaspis* would become paraphyletic if species other than the type species were included in it. For this reason, the reference to '*Zenaspis*' of the species *Cephalaspis metopias* Wängsjö (1952) from Spitsbergen, and one of the two species from Podolia described below, is only provisional until the interrelationships of these advanced scolenaspidians are revised in detail. This uncertainty of the monophyly of *Zenaspis* is expressed by a polychotomy in Fig. 4, p. 315.

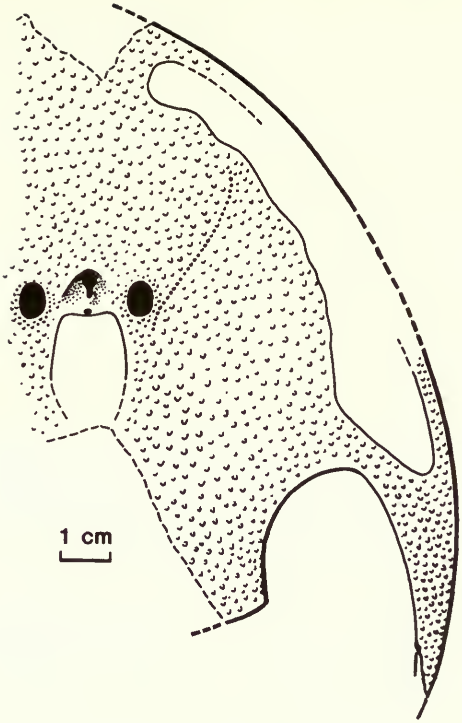

Fig. 13 *Zenaspis podolica* (Balabai), 'Old Red' I, Lower Devonian, Ustečko, Podolia, Ukrainian S.S.R. Based on P.17713.

'*Zenaspis*' *podolica* (Balabai)
Fig. 13

1962 *Cephalaspis podolica* Balabai: 4; fig. 4.

Diagnosis (emended). Relatively large *Zenaspis*-like species, with medially curved cornual processes. Pineal plate fused laterally with the orbital margin. Exoskeleton ornamented with large, single tubercles.

Holotype. Specimen no. 23562 of the Museum of the Academy of Sciences of the Ukrainian S.S.R.; probably 'Old Red' I, Ustečko, Podolia, Ukrainian S.S.R.

Material. Ustečko (Uscieszko): BM(NH) P.17713, labelled by Zych as '*Cephalaspis salweyiformis*'.

Remarks. This species is the only one which has been adequately figured by Balabai (1962: fig. 4), and can be compared with the material in the British Museum (Natural History). I refer to it an imperfect shield (P.17713), which resembles the holotype and came from the same locality. However, a number of large scolenaspidian shield fragments with large tubercles probably also belong to this species.

'*Z.*' *podolica* resembles '*Z.*' *metopias* from Spitsbergen in the reduction of the pineal plate, and the fusion of its lateral parts with the orbital margin, a character also met with in some *Machairaspis* species, as well as in *Tegaspis* and *Diademaspis*. The lateral fields are also similar in shape in the two species, but the cornual processes are much longer in '*Z.*' *podolica*.

Zenaspis cf. ***salweyi*** (Egerton)
Fig. 14

A number of shields in the collection of the British Museum (Natural History) have been labelled by Zych as '*Cephalaspis salweyi* var. *podolica*'. They differ from '*Z.*' *podolica* in

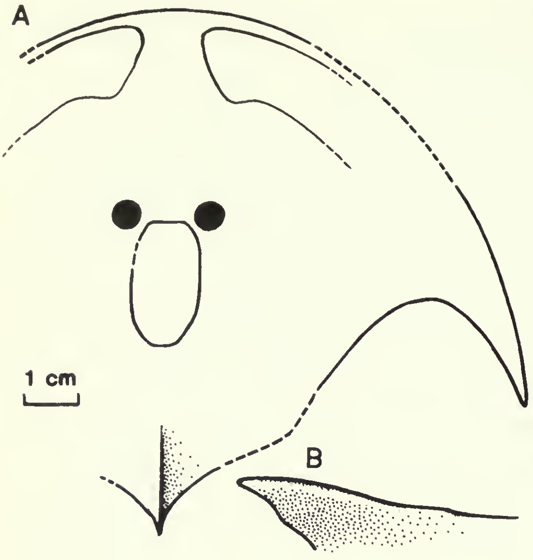

Fig. 14 *Zenaspis* cf. *salweyi* (Egerton), 'Old Red' II, Gorodnica, Podolia, Ukrainian S.S.R. Specimen P.20490. A, dorsal view; B, lateral view of the spinal process.

being smaller but have very much the same type of ornamentation. This Podolian material cannot be specifically identified with the type material of *Z. salweyi* from Great Britain, because the latter species is defined mainly by its overall shape and size, and no specimen from Podolia is well enough preserved to allow for detailed comparisons. It is thus preferable to refer to the Podolian material as *Z.* cf. *salweyi.* Among the best-preserved specimens, BM(NH) P.20526–7 is almost identical to the specimens of *Z. salweyi* from Great Britain.

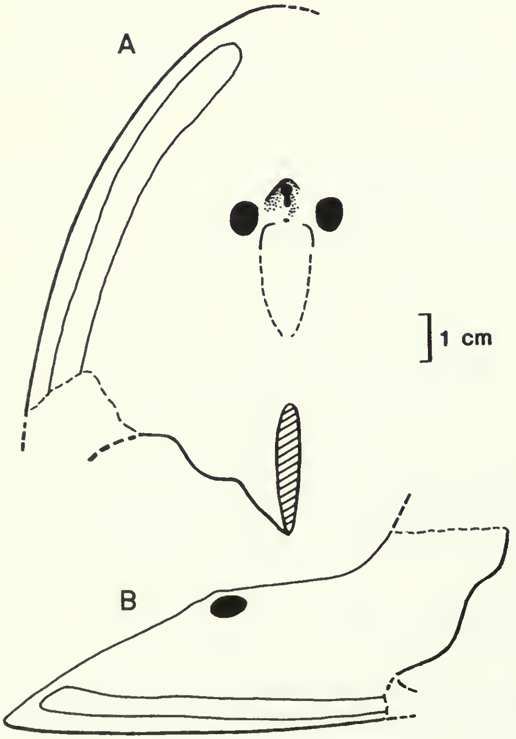

Fig. 15 *Machairaspis* sp., 'Old Red', Gorodnica, Podolia, Ukrainian S.S.R. Specimen P.17720, labelled by Zych as '*Cephalaspis salweyi* var. *podolica*'.

Specimen BM(NH) P.20490–1 (Fig. 14) is also referred here to *Z.* cf. *salweyi*, but differs from the others in its sightly more expanded shield and in its broad lateral fields. However, this difference may be due to a distortion of the fossil.

MATERIAL. Gorodnica (Horodnica) N II: BM(NH) P.20426–7, P.20463, P.20490–1, P.20494, P.20515; Ustečko (Uscieszko): P.20532–3, P.20536–7, P.20538.

Genus *MACHAIRASPIS* Janvier 1980

TYPE SPECIES. *Cephalaspis corystis* Wängsjö (1952); east side of Red Bay, north-west Spitsbergen.

Machairaspis sp.
Fig. 15

The specimen BM(NH) P.17720, labelled by Zych as '*Cephalaspis salweyi* var. *podolica*' differs from *Z.* cf. *salweyi* in its elongate shield and its much larger dorsal spinal process on the abdominal division. It is very similar to some of the species I referred to the genus *Machairaspis* (*M. corystis, M. ibex, M. battaili, M. hastata*; Janvier 1980). The dorsal spinal process is not preserved but its base is elongate, as in *M. corystis* or *M. battaili* (Wängsjö 1952: fig. 52; Janvier 1980: fig. 163). The lateral fields are relatively narrow, as is usual in the species of this genus. This specimen is from Gorodnica N II, and probably comes from the 'Old Red' I or II.

Genus *DIADEMASPIS* Janvier 1980

DIAGNOSIS. Medium-sized to very large scolenaspidians with very large hypophysial division of the nasohypophysial opening, and with an ornamentation of clusters of large tubercles in the centre of each tessera. Pectoral sinuses situated far back. Cornual process short.

TYPE SPECIES. *D. poplinae* Janvier (1980); James I Land, Spitsbergen.

REMARKS. The generic name was erected for huge scolenaspidians from the upper part of the Wood Bay Formation of Spitsbergen (namely *D. poplinae* Janvier 1980: 263, '*C.*' *jarviki* Wängsjö 1952: 378, and '*C.*' *fracticornis* Wängsjö 1952: 385). Some of the species of this genus have an extremely enlarged hypophysial division; in *D. poplinae*, for instance, it is almost as large as the orbits (Janvier 1980: fig. 156). The ornamentation of most *Diademaspis* species is quite characteristic, and can easily be recognized on small exoskeleton fragments. A character *Diademaspis* shares with *Zenaspis* and *Tegaspis* is the broad posterior part of the lateral fields, produced medially into a small lobe. It shares also with some '*Zenaspis*' species the fusion of the lateral part of the pineal plate with the orbital margin. Whether this latter character can be regarded as a synapomorphy is uncertain because it is known to occur also in some species of *Machairaspis*, as well as, probably, in *Tegaspis*, and it is likely that this modification of the pineal plate took place independently in several subgroups of the scolenaspidians and perhaps also in other osteostracan groups.

Diademaspis sp.
Fig. 16

Some fragmentary shields of large scolenaspidians from Podolia show the typical ornamentation of *Diademaspis*; that is, clusters of large tubercles in the centres of the tesserae. In some of them, the lateral fields are partly visible, and they have exactly the same shape as in *D. poplinae* Janvier, from the Kapp Kjeldsen, Lykta and Stjørdalen Divisions of the Wood Bay Formation of Spitsbergen. None of these specimens is complete enough to allow detailed comparisons with the species known from Spitsbergen.

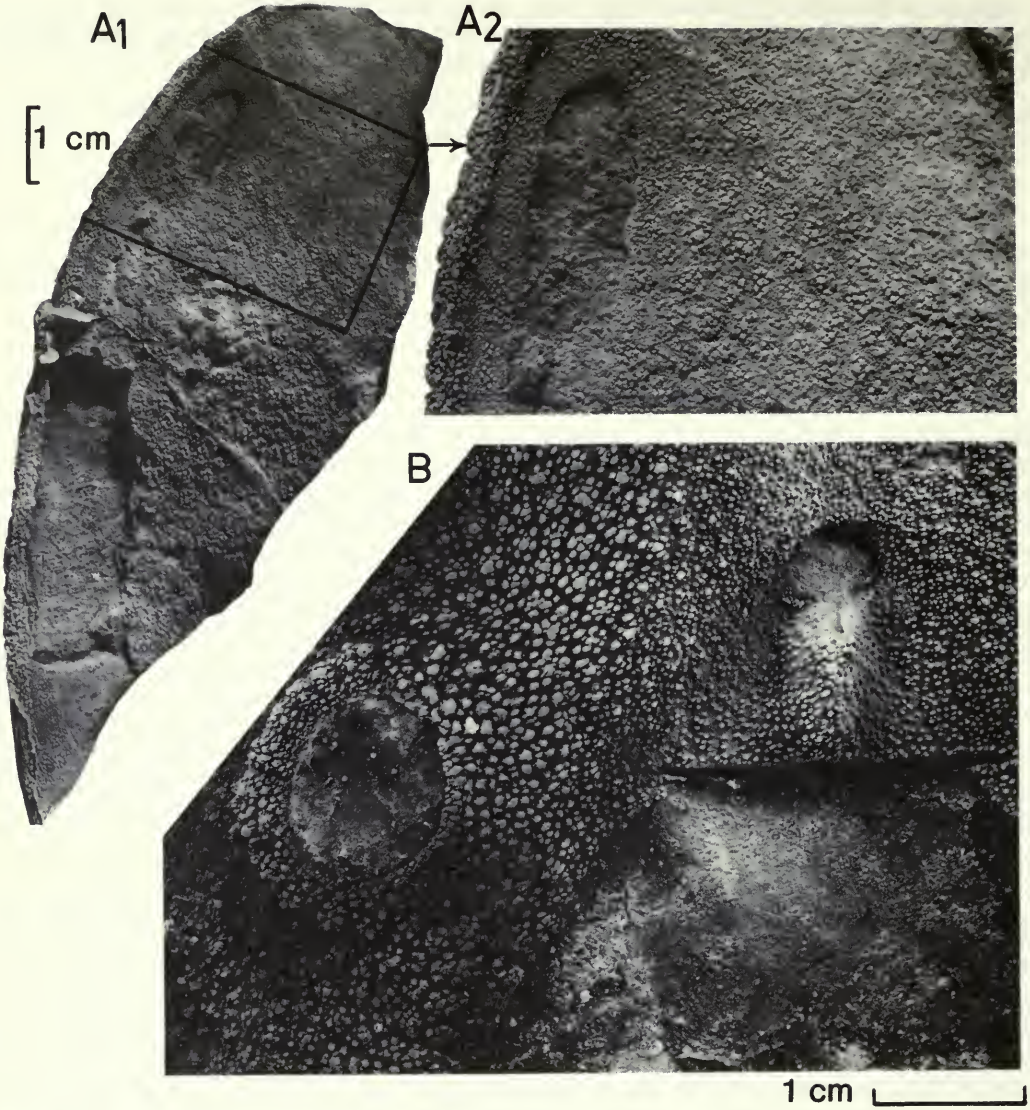

Fig. 16 A, *Diademaspis* sp., 'Old Red' ?, Ustečko, Podolia, Ukrainian S.S.R. Specimen P.17729, labelled by Zych as '*Cephalaspis tesseyrei*'. Latex cast of the anterodorsal part of the shield (A1) and enlarged view of the ornamentation (A2). B, *Diademaspis* sp., Wood Bay Formation, Lykta Division, Wagnerfjellet, Spitsbergen; specimen in Muséum National d'Histoire Naturelle, Paris (SVD 1108), showing the orbitotemporal and nasohypophysial regions of the shield.

Material. Červonograd (Czerwonogrod) N: BM(NH) P.17729 (labelled by Zych as '*Cephalaspis teisseyrei*'), probably from the 'Old Red'; Ustečko (Uscieczko): BM(NH) P.17727 (labelled by Zych as '*Cephalaspis mornewieczi*', probably from the 'Old Red' or Ivanie horizon). The specimen C.85 of the Naturhistoriska Riksmuseet, Stockholm, had been labelled by Zych as the holotype of '*C. teisseyrei* var. *major*', but it is uncertain whether specimen BM(NH) P.17729 can be assigned to Zych's *C. teisseyrei* var. *major*.

INCERTAE SEDIS

The Podolian material in the British Museum (Natural History) includes a large number of shield fragments which can be referred to scolenaspidians on account of the ornamentation and the shape of the cornual processes and lateral fields, but which cannot be assigned to any particular genus, either because they show too generalized features of the group or because they are too fragmentary.

'*Scolenaspis*' *mikrolepidota* (Balabai)

1962 *Cephalaspis mikrolepidota* Balabai: 6; fig. 8.

Balabai gave a relatively good figure of the type specimen of this species, which seems to be a scolenaspidian, recognizable by the shape of its lateral fields and spinal process. The shield is elongate in shape, as in *Machairaspis*, but the spinal process does not seem to be as large as in the latter genus. For the moment, it is preferable to refer to this species as '*Scolenaspis*' *mikrolepidota* to suggest its scolenaspidian affinities and also its primitive condition within the group. The type specimen, no. 17323 of the Museum of the Academy of Sciences of the Ukrainian S.S.R., is from Ustečko and comes probably from the 'Old Red'.

There are a number of specimens in the collection which can be identified as scolenaspidians, but for which no more precise information can be given: P.20485 – cornual process, Gorodnica N II; P.20427 – imperfect low cephalic shield, Gorodnica W II; P.20528 – imperfect shield, Gorodnica W II; P.20569 – cornual process, Gorodnica W Ia; P.20572 – cephalic shield resembling that of *Z. salweyi*, Gorodnica S.

CEPHALASPIDIANS

The cephalaspidians comprise at least the genera *Cephalaspis* s.str. and *Meteoraspis*, but the genera *Pattenaspis, Mimetaspis* and *Hildenaspis* are provisionally regarded as cephalaspidians on the basis of the shape of the first '*s.e.l.*' canal, which is also geniculated, However, this group deserves a careful revision and may turn out to be paraphyletic. The cephalaspidians are relatively rare in the Podolian material, and the few species of that group which can be recognized show mainly generalized characters; that is, medium-sized shield with no conspicuous ornamentation, short abdominal division, and short and flattened cornual processes with lateral fields extending posteriorly onto their dorsal surface. Apart from one species which is referable to the genus *Mimetaspis*, the other cephalaspidians from Podolia are referred to here as '*Cephalaspis*' but must be regarded as *incertae sedis* within the group.

Genus ***MIMETASPIS*** Stensiö 1958

DIAGNOSIS. Small to medium-sized cephalaspidians with no independent pineal plate, short cornual processes and almost smooth surface of the exoskeleton. Median dorsal field anteriorly pointed. Orbits relatively large.

TYPE SPECIES. *Cephalaspis hoeli* Stensiö (1927); Ben Nevis, north-west Spitsbergen.

REMARKS. The generic name *Mimetaspis* was erected by Stensiö (1958) for *Cephalaspis hoeli* Stensiö (1927) which was considered to differ from the 'typical' *Cephalaspis* species in the orthobranchiate condition of the oralobranchial chamber. Although this latter character cannot be upheld (Janvier 1980: 163), the generic name *Mimetaspis* can be used for *C. hoeli, C. exilis* Wängsjö, and some other species from Spitsbergen and Podolia, which form a monophyletic group in which the pineal plate is no longer independent and the ornamentation of the exoskeleton consists of very small elongate tubercles which are only visible under the microscope.

Mimetaspis glazewskii sp. nov.
Figs 17, 18

Diagnosis. Large *Mimetaspis* species with relatively broad anterior end of the median dorsal field.

Holotype. BM(NH) P.20958–9, labelled by Zych as '*Cephalaspis glazewskii*'; Ivanie horizon or 'Old Red' I, Ustečko (Uscieszko) W, Podolia, Ukrainian S.S.R. Fig. 18.

Name. After Mr K. Glazewski, of the University of L'vov.

Material. Holotype; Ustečko (Uscieczko): P.20961–4.

Remarks. The general shape of the shield resembles that of *M. hoeli* (Stensiö 1927, Wängsjö 1952), but differs from it in its larger size and the broader anterior end of the median dorsal

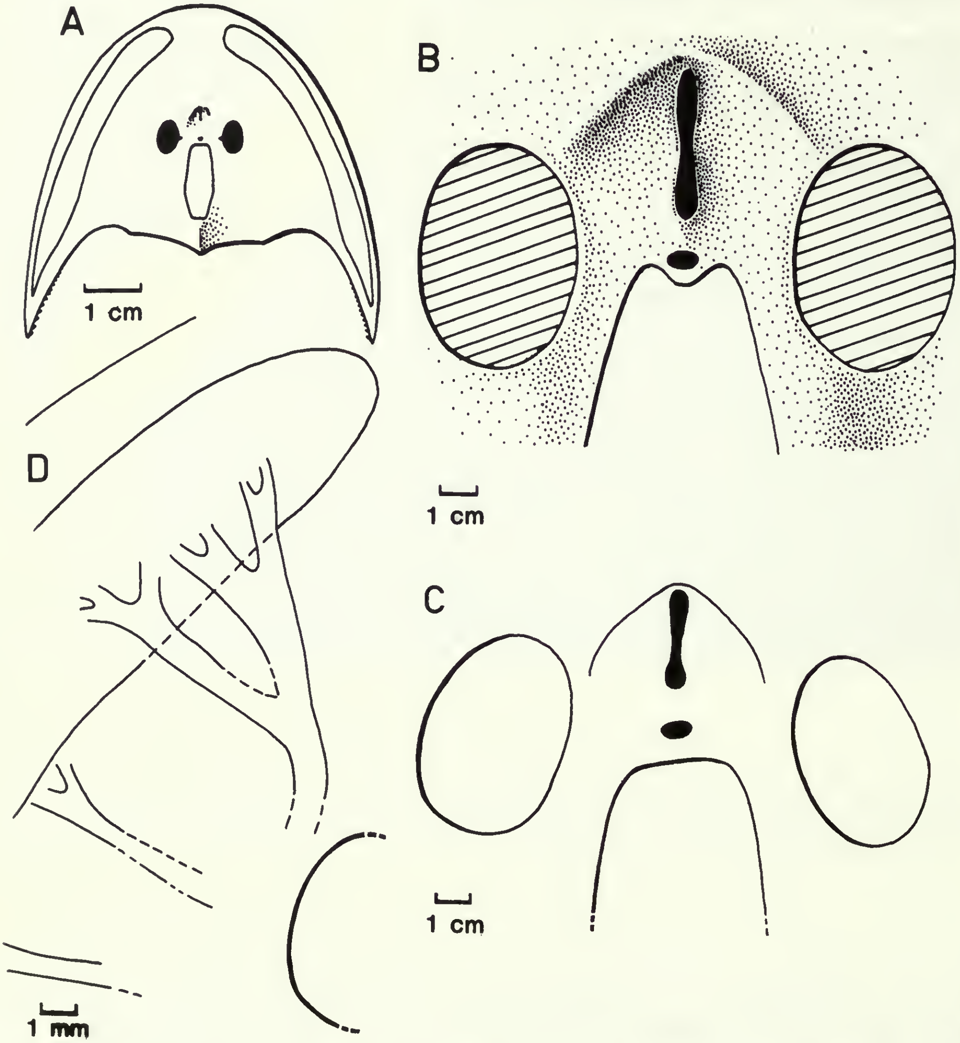

Fig. 17 *Mimetaspis glazewskii* sp. nov., 'Old Red' I or Ivanie horizons, Ustečko, Podolia, Ukrainian S.S.R. A, reconstruction of the shield based on the holotype (P.20958–9), dorsal view. B, C, orbitopineal and nasohypophysial regions of the shield, based on the holotype (B) and P.20961–4 (C). D, first '*s.e.l*' canal of the left side in P.20961.

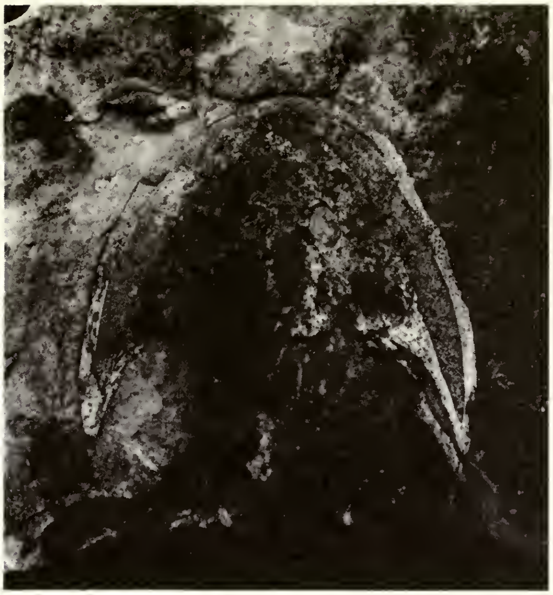

Fig. 18 *Mimetaspis glazewskii* sp. nov., Ivanie horizon, 'Old Red' I, Ustečko (Uscieszko) W, Podolia, Ukrainian S.S.R. **Holotype** (part, P.20958), dorsal view. × 0·85.

field. The surface of the exoskeleton is covered with extremely small (about 0·05 mm) and elongate tubercles of the same type as in *M. hoeli* and *Hildenaspis digitalis* Janvier (1976). The lateral fields have regular limits and extend far backwards onto the dorsal face of the cornual processes, as is usual in cephalaspidians. The cornual processes are broad and flattened and bear minute denticles on the medial edge. The abdominal division is very short, with a faint median elevation. The median dorsal field is narrow anteriorly but slightly broader than in other species of the same genus, and sends off two 'horns' on each side of the pineal foramen (Fig. 17B). In some specimens (Fig. 17C) the anterior end of the median dorsal field is blunt and situated far behind the pineal foramen. There is no trace of an independent pineal plate and there is no indication as to how it had become fused or reduced. The two divisions of the nasohypophysial opening are equal in size, as in most cephalaspidians and non-cornuate osteostracans (Fig. 17B, C).

In BM(NH) P.20961 (Fig. 17D), the first '*s.e.l.*' canal can be traced and it branches at a point half way between the orbit and the lateral field, bending strongly at this point. This is regarded as a common feature of cephalaspidians.

M. glazewskii is larger than any of the other *Mimetaspis* species, but its size fits that of some shield fragments referred to *Mimetaspis* sp. from the base of the Wood Bay Formation of Spitsbergen.

INCERTAE SEDIS

'Cephalaspis' rogalai Balabai

Fig. 19A

1962 *Cephalaspis rogalai* Zych *in* coll.; Balabai: 3, fig. 1a, b.

This species is known from Ostrovčik (Ostrowczyk, north of Džurin, on the Džurin river), Ustečko (Uscieszko), Gorodnica (Horodnica) and Džurin (Djurin). It is somewhat smaller than *M. glazewskii* and its shield is more elongate in shape. It may also belong to the genus *Mimetaspis*, but the figure given by Balabai is too imprecise to be certain. If the presence of

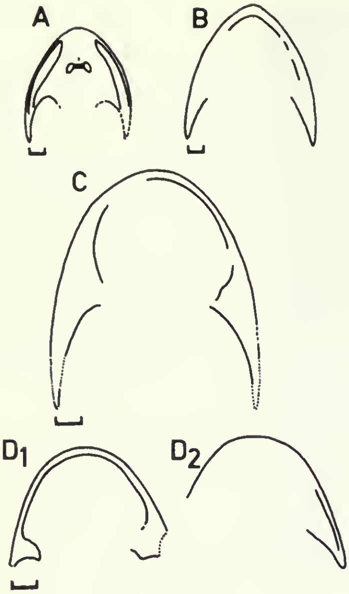

Fig. 19 A, '*Cephalaspis*' *rogalai* Balabai, 'Old Red', Ustečko, Gorodnica, Podolia, Ukrainian S.S.R. B, '*Cephalaspis*' *feliciae* Balabai, 'Old Red', Bilomu bridge, Podolia, Ukrainian S.S.R. C, '*Cephalaspis*' *major* Balabai, 'Old Red', Gorodnica, Podolia, Ukrainian S.S.R. Specimen 25579, Museum of the Ukrainian Academy of Sciences, L'vov. D, '*Cephalaspis*' *sjoestremi* Balabai, 'Old Red', Ustečko, Ruzdviani and Kijdanov (the two latter localities are on the Strypa river, north of Bučač), Podolia, Ukrainian S.S.R. (all after Balabai 1962). Scale bars all 1 cm.

a pineal plate and the ogive-like rostral margin described by Balabai are correct, then it may also be suggested that this species belongs to the genus *Pattenaspis*.

In the British Museum (Natural History) collections, some specimens (e.g. P.17712) from Ustečko W. have been labelled by Zych as '*Cephalaspis rogali*' (*sic*), but they are only undeterminable cephalaspidian fragments.

'*Cephalaspis*' *feliciae* Balabai
Fig. 19B

1962 *Cephalaspis feliciae* Balabai: 4; fig. 2.

This species, from Bilomu bridge (north of Bely Potok, on the Seret river) is poorly known and I regard it as a *nomen dubium*.

'*Cephalaspis*' *major* Balabai
Fig. 19C

1962 *Cephalaspis major* Balabai: 4; fig. 3.

This remarkably large species, from Gorodnica and Ivanie, has slender cornual processes. It is uncertain whether it is a cephalaspidian or a scolenaspidian.

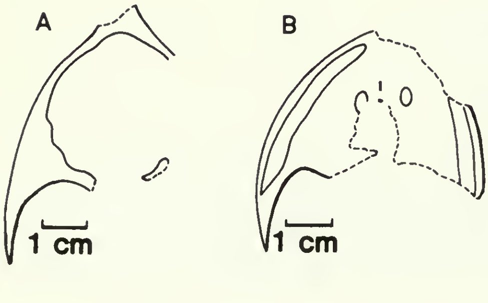

Fig. 20 A, '*Cephalaspis*' cf. *acutirostris* Stensiö, 'Old Red', Gorodnica, Podolia, Ukrainian S.S.R. Specimen P.20508, ventral view. B, undetermined cephalaspidian, 'Old Red', Gorodnica, Podolia. Specimen P.20498, dorsal view.

'Cephalaspis' sjoestremi Balabai
Fig. 19D

1962 *Cephalaspis sjöstremi* Balabai: 5; fig. 5.

This species is from Ustečko, Rizdvano (Ruzdwiany) and Kijdanov (Kujdanow), the two latter localities being on the Strypa river, north of Bučač. it resembles '*C.*' *kozlowskii* in the outline of the shield (Fig. 19D). A *nomen dubium.*

'Cephalaspis' kozlowskii Zych

1937 *Cephalaspis kozlowskii* Zych: 63; pls 1–4.

This species is known from Zaleščiki (Zaleszczyki) and Vorvolinče (Worwolincze) where it occurs in the Ivanie horizon and the 'Old Red' I (Karatayute-Talimaa 1981: table 7). The internal anatomy has been described in detail by Zych (1937) but the central part of the shield and the shape of the nasohypophysial opening are unknown. However, the shape of the lateral fields, the cornual processes, and the mode of branching of the first '*s.e.l.*' canal (Zych 1937: pl. 2) incline me to consider it a cephalaspidian, although features of the oralobranchial chamber (branchial impressions, well-marked interbranchial ridges and nerve and blood vessel impressions) suggest scolenaspidian affinities. If it is a scolenaspidian, it must be a primitive form, like '*C.*' *pagei* or '*C.*' *powriei.* '*C.*' *kozlowskii* well illustrates the problem of the limits of the scolenaspidians and the cephalaspidians, a re-examination of which may show that some of the so-called cephalaspidian or scolenaspidian characters are only those of primitive cornuate osteostracans. I suspect that the flattened cornual processes and the narrow lateral fields are such characters, and this would explain why they occur also in the most primitive scolenaspidians.

'Cephalaspis' cf. *acutirostris* Stensiö
Fig. 20A

Specimen BM(NH) P.20508–9, from Gorodnica N ('Old Red' II), is very similar to the holotype of '*C.*' *acutirostris* (Stensiö 1932: fig. 32; pl. 40, fig. 13) from the Lower Old Red Sandstone of Shropshire. However, since the dorsal face of the shield is not known in either specimen it is uncertain whether this resemblance is superficial or not. In both specimens the rostral process is broken off and only its proximal part is known. The only difference between the Podolian specimen and the holotype is that the cornual processes are broader in the former than in the latter.

Undetermined Cephalaspidians

BM(NH) P.17726 – This specimen from Bely Potok (Potok Bialy) has been labelled by Zych as '*Cephalaspis potokiensis*', but I regard it as an undetermined cephalaspidian.

BM(NH) P.20498–9 – This specimen (Fig. 20B) from Gorodnica may belong to the genus *Mimetaspis*, but is too distorted to allow closer determination.

UNDETERMINED OSTEOSTRACANS

Besides a number of undeterminable osteostracan fragments which are too badly preserved to assign to any of the species mentioned above, there are two specimens which certainly do not belong to any of the species hitherto described from Podolia but which are too poorly preserved to be described as new taxa.

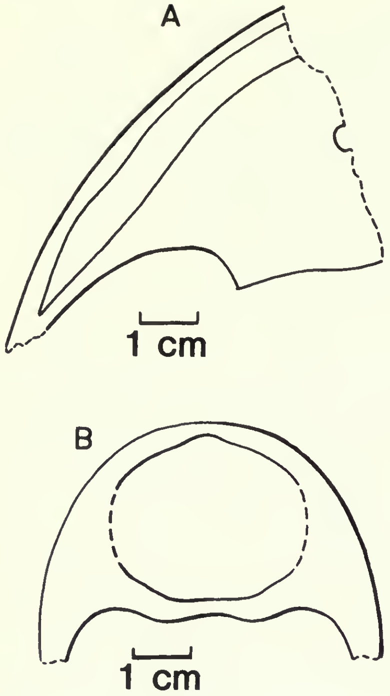

Fig. 21 A, specimen P.17722, labelled by Zych as '*Cephalaspis arnelli*', 'Old Red' ?, Potokčiska, Podolia, Ukrainian S.S.R. B, ? benneviaspidian, 'Old Red', Gorodnica, Podolia, Ukrainian S.S.R. Specimen P.20518.

BM(NH) P.17722 – This shield fragment (Fig. 21A) from Potoczyska N has been labelled by Zych as '*Cephalaspis arnelli*', a species name found also on the label of specimen C.129 in the Naturhistoriska Riksmuseet, Stockholm. The latter specimen closely resembles *Z. salweyi*, but is somewhat smaller and has posteriorly narrower lateral fields extending onto the cornual processes.

BM(NH) P.20518 – This is the ventral rim of a small shield (Fig. 21B) from Gorodnica N ('Old Red' I); it is suggestive of a primitive benneviaspidian because of its regularly rounded marginal region. It is the only possible benneviaspidian specimen from Podolia in the British Museum (Natural History) collection.

Faunal comparisons and Stratigraphical remarks

The osteostracan fauna described here on the basis of the British Museum (Natural History) material can be considered as coming from the Ivanie horizon and, mainly, from the 'Old Red' I and II. The nature of the sediment in which the specimens are preserved suggests that none of them comes from the Čortkov and Borshchov horizons. Comparisons can be carried out with the faunas from the Devonian of the Anglo-Welsh area and Spitsbergen.

Two aspects of the Podolian fauna are particularly striking: the lack of *Meteoraspis* (and the rarity of the cephalaspidians in general) and the abundance of the scolenaspidians. This is true for all the localities cited in this paper. The benneviaspidians are also rare, although the more recently collected material in the Palaeontological Institute of the Academy of Sciences of the U.S.S.R. contains several well-preserved large benneviaspidians (Karatayute-Talimaa, personal communication). The kiaeraspidians and thyestidians are totally absent. The large scolenaspidians (*Zenaspis* cf. *salweyi*, '*Z.*' *podolica*) compare satisfactorily with species from the top part of the Red Bay Group of Spitsbergen (Ben Nevis Formation) such as '*Z.*' *metopias*. The association of *Z.* cf. *salweyi* and *Stensiopelta pustulata* is also very suggestive of that of *Z. salweyi* and *S. woodwardi* in the 'Dittonian II' of Wales (Stensiö

1932: 199–202). The few fragments referable to *Diademaspis* do not reach the size of the huge specimens which occur in the upper part of the Wood Bay Formation of Spitsbergen.

As far as the osteostracan fauna is concerned, the lowest formations of the Red Bay Group of Spitsbergen are characterized by the abundance of small cephalaspidians such as *Pattenaspis* and *Mimetaspis*. These small forms become rare in the Ben Nevis Formation (with *M. hoeli* only) and in the Wood Bay Formation. In Podolia, there seems to be only one or two species of *Mimetaspis* resembling *M. hoeli*.

The osteostracan fauna of the Podolian 'Old Red' and Ivanie horizon does not contain the classical taxa of the Wood Bay Formation, but contains taxa which are suggestive of those of the upper part of the Red Bay Group of Spitsbergen, and those of the 'Dittonian II' of Great Britain.

Acknowledgements

I wish to express my gratitude to the Keeper of Palaeontology and Dr Peter Forey for having given me access to the collections of the British Museum (Natural History), and to the latter for having improved and commented on the manuscript of this paper. I thank also Professor Tor Ørvig (Stockholm) for letting me study the Podolian material at the Naturhistoriska Riksmuseet.

For providing me biographical data on W. Zych, I am particularly indebted to Dr Wit Tarnawski and Mrs Maria Tarnawska of Monmouth, Dr Zofia Kielan-Jaworowska of Warsaw and the late Professor Stensiö. I thank also Mr A. Zalk for translations from Polish to French.

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Hipparion sp. (Equidae, Perissodactyla) from Diavata (Thessaloniki, northern Greece)

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Synopsis

Some hipparion remains from Diavata, about 4 km NNW of Thessaloniki, northern Greece, are studied; the locality is known for the giant hyaena *Hyaena salonicae* Andrews. The hipparion is medium to large, and has highly plicated teeth, a large subtriangular protocone, usually multiple 'plis caballins' and an elliptical hypocone with two hypoconal grooves. It represents a form between the primitive hipparions of the Lower Vallesian and the more evolved ones of the Turolian. It belongs to the second *Hipparion* zone of the Mediterranean Neogene, of Upper Vallesian–early Lower Turolian age. No specific name is given because of the small amount of material and the unknown locality.

Introduction

Some hipparion specimens similar to *Hipparion gracile* (Kaup) from the village of Diavata (Dudular), near Thessaloniki, are examined. The material was briefly described by Andrews (1918). The large hyaena *Hyaena salonicae* Andrews is believed to come from the same locality, because of its similar fossilization, but the provenance of the hipparion is more certain ('. . . village Diavata NNW of Salonica . . .') than that of the hyaena ('. . . near Salonica . . .') (Andrews 1918).

There are many papers which discuss the hyaena and its age, but no data concerning the hipparion have yet been published, although they are useful in dating the locality. The hipparion material is described and compared with material coming from the Thessaloniki area (lower Axios valley) and from other Greek and Eurasiatic localities.

Locality

The exact position of the Diavata locality (the old name Dudular has lapsed) is unknown and our efforts to find it are still unsuccessful, because new buildings in the area have changed the terrain. The locality was found in 1917 by Captain Seymour W. Davies, R.A.M.C., who collected the only known material, now stored at the British Museum (Natural History). Information about the site and the deposits are contained in a letter from the collector to Dr L. Fletcher, Director of the BM(NH).

The locality must lie in one of the ravines NE of the village of Diavata between the Gallikos river and the hill Tris Toumbes (Fig. 1). Traces of matrix found on the fossils suggest the fossiliferous bed consists of a yellowish, hard, sandy material, but the collector says in his letter that the fossils occurred in a stiff stratified clay; the fossiliferous deposit is thus most likely a sandy marl. At the bottom of the ravine he said there was a hard (sandy?) conglomerate under the fossiliferous bed, and overlying the fossiliferous bed a series of clay or sand alternating with fine sands or with larger pebbles (Capt. Davies' letter).

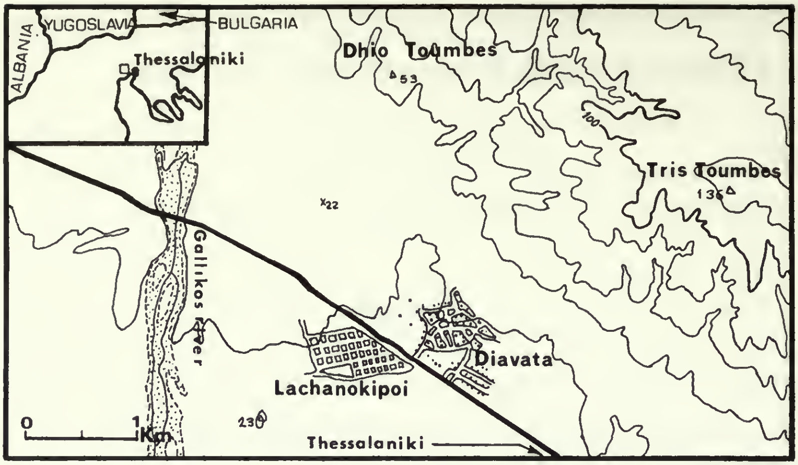
The well-known continental neogene deposits of the neighbouring lower Axios valley (Arambourg & Piveteau 1929) consist of three series (Bonis *et al.* 1977, Koufos 1980):

i. a series of yellowish marls, gravels, sands and sandy marls of Dytiko (Upper Turolian),

ii. a series of white-yellow sediments (sandy marls, gravels, sands, marls) of Vathylakkos (Lower Turolian), and

Bull. Br. Mus. nat. Hist. (Geol.) **38** (5): 335–345

Issued 31 January 1985


YUGOSLAVIA
BULGARIA
ALBANIA
Thessaloniki
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Tris Toumbes
136
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Gallikos River
Diavata
Lachanokipoi
23
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Thessaloniki

Fig. 1 Map of the Diavata area.

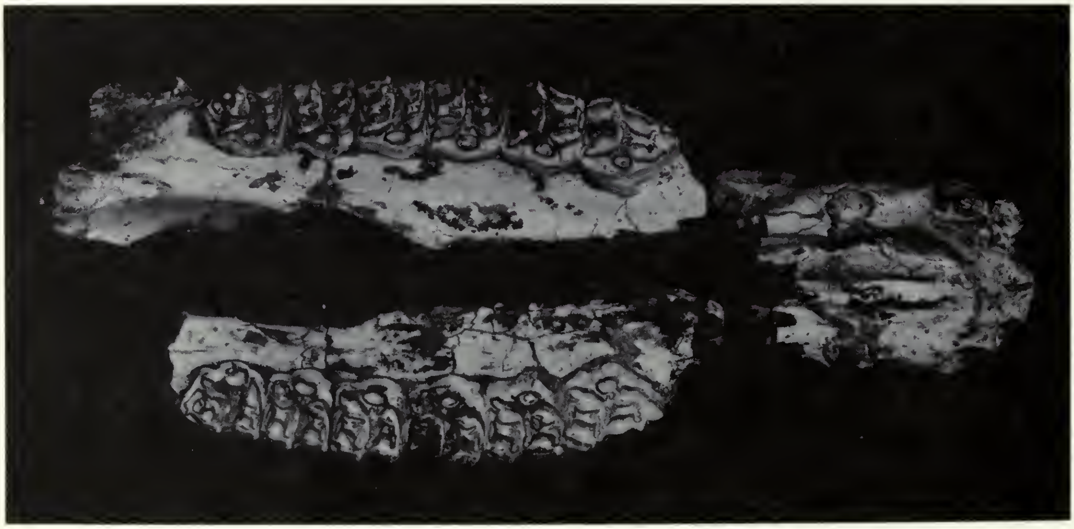

Fig. 2 *Hipparion* sp. BM(NH) M.11585a–c. Diavata, Thessaloniki, Greece. × 0·4. Photo. BM(NH).

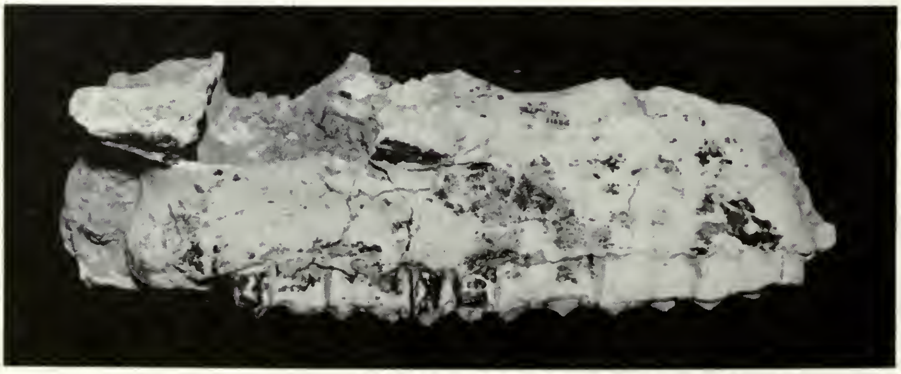

Fig. 3 *Hipparion* sp., right maxilla. BM(NH) M.11585a, lateral view. Diavata, Thessaloniki, Greece. × 0·5.

iii. very hard red beds and yellowish marls of Nea Mesimvria (Upper Vallesian–early Lower Turolian).

Thus if Capt. Davies' description of his deposits is accurate they are similar to those of the lower Axios valley. Accordingly the stratigraphy of the locality must be:

i. clay or sand alternating with beds of fine sand or large pebbles,
ii. a yellowish, hard and stratified, sandy marl with the fossils, and
iii. a hard conglomerate, at the bottom of the ravine.

Material and Measurements

All measurements are in mm with estimated values in brackets. Tooth-series length is measured at alveolar level. DAP = anteroposterior diameter; DT = transverse diameter. See also Table 1. Dental nomenclature is according to Sondaar (1961).

1. Right maxilla with P^2–M^3, BM(NH) M.11585a:
   Length P^2–M^3 = 149·0
   Length P^2–P^4 = 79·0
   Length M^1–M^3 = 70·0
2. Left maxilla with P^2–M^3, BM(NH) M.11585b:
   Length P^2–M^3 = 150·0
   Length P^2–P^4 = 80·0
   Length M^1–M^3 = 69·9
3. Portion of premaxillae with left I^2–I^3 and right I^2, BM(NH) M.11585d:
   Width at the border of the incisors = 60·0
4. Portion of premaxillae without incisors, BM(NH) M.11585c:
   DAP I^3–C = 20·9
   Width at the border of the incisors = 61·0
5. Occipital portion of a skull, BM(NH) M.11585e:
   Foramen magnum: Height = 40·0
   Foramen magnum: Width = 29·0
   Max. width between the external surfaces of the condyles = 78·0
6. Proximal part of a radius with remains of diaphysis of the ulna, BM(NH) M.11586a:
   $DT_{prox.}$ = 66·3
   $DT_{prox.\ art.\ surf.}$ = (63)
   $DAP_{prox.\ art.\ surf.}$ = 31·0
7. Distal part of a tibia, BM(NH) M.11586b:
   $DT_{dist.}$ = 61·3
   $DT_{dist.\ art.\ surf.}$ = 50·7
   $DAP_{dist.}$ = 38·5
8. Proximal and distal part of a tibia from a young individual, BM(NH) M.11586c, d.

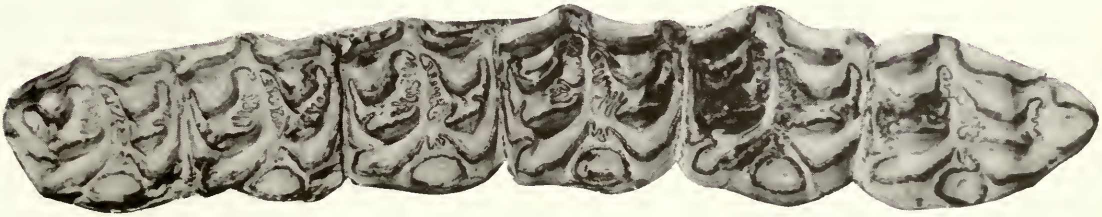

Fig. 4 *Hipparion* sp., right tooth-series. BM(NH) M.11585a, occlusal view. Diavata, Thessaloniki, Greece. × 0·95.

Table 1 Tooth measurements (mm) in the Diavata hipparion.

Teeth		DAP × DT (occlusal)	DAP × DT protocone	Enamel formula[1]	Protocone shape index[2]
P^2	right	30·0 × 23·6	7·2 × 5·4	$\frac{4, 8, 5, 2}{1}$	75
	left	31·0 × 23·5	7·4 × 5·7	$\frac{6, 9, 7, 2}{1}$	77
P^3	right	24·5 × 25·8	7·6 × 5·1	$\frac{5, 8, 7, 2}{1}$	67
	left	24·5 × 25·3	7·7 × 5·2	$\frac{3, 10, 9, 1}{1}$	67
P^4	right	25·0 × 25·3	8·0 × 5·6	$\frac{3, 11, 10, 2}{3}$	70
	left	24·9 × –	8·0 × 5·3	$\frac{2, 8, 8, 1}{2}$	66
M^1	right	20·9 × 23·0	7·8 × 4·8	$\frac{2, 9, 11, 1}{3}$	61
	left	20·7 × 24·1	8·0 × 4·9	$\frac{2, 9, 13, 2}{5}$	61
M^2	right	21·2 × 23·0	7·9 × 4·9	$\frac{3, 10, 9, 2}{2}$	62
	left	21·5 × 24·0	8·0 × 4·8	$\frac{2, 8, 11, 2}{2}$	60
M^3	right	24·8 × 21·6	7·8 × 4·5	$\frac{3, 7, 7, 4}{3}$	58
	left	25·2 × –	7·5 × –	$\frac{4, 7, 8, 3}{2}$	–

[1,2] Gromova (1952).

Description

The two maxillae studied do not preserve large parts of the skull. The crista facialis of the right maxilla is well preserved; its anterior end is above the M^1 and its distance above the alveolus of the M^3 is 41·0 mm. The teeth are well preserved except for the P^4, M^1 and M^3 of the left maxilla, which are partly destroyed. The wear of the teeth is at the end of the second stage or beginning of the third (Gromova 1952).

P^2: Small with a short anterostyle relative to length. The fossettes are closed, unconnected and highly plicated along their front and rear borders; the plications in their borders are not very deep and the enamel is thin. The 'bouclé prefossette' is multiplicate. The protocone is elliptical and connected with the protoloph. The hypocone is elliptical and has a hypoconal groove which is narrow and deep distally and rudimentary lingually. The 'pli caballin' is simple and well developed.

$P^{3,4}$: The fossettes are unconnected, closed and with high enamel plication. The 'bouclé prefossette' in the right P^4 is separated as an islet. The protocone is large, subtriangular and

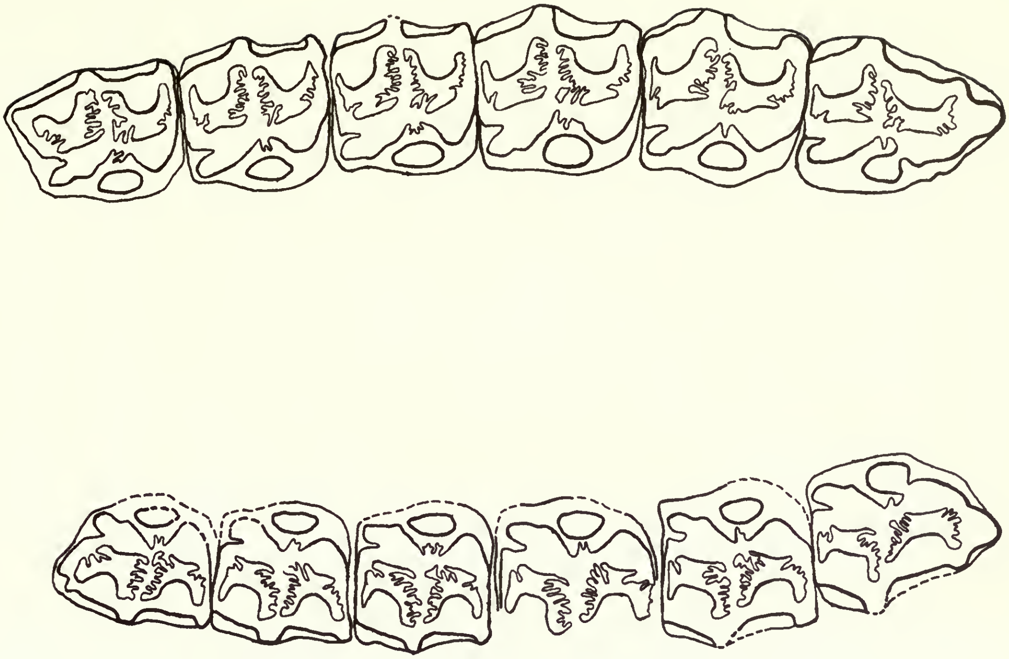

Fig. 5 Tooth-series of the Diavata *Hipparion*. × 0·85.

isolated from the protoloph. The 'pli caballin' is simple in the P^3, and double or triple in the P^4. The hypocone is elliptical and angular posteriorly with two hypoconal grooves.

$M^{1,2}$: These are smaller than the premolars but with the same morphology. The prefossette of both the M^2 is open at the 'bouclé prefossette', which has almost disappeared. The protocone is elongated, subtriangular and isolated from the protoloph. The 'pli caballin' is multiple in the M^1 and double in the M^2. The hypocone is like that in the $P^{3,4}$.

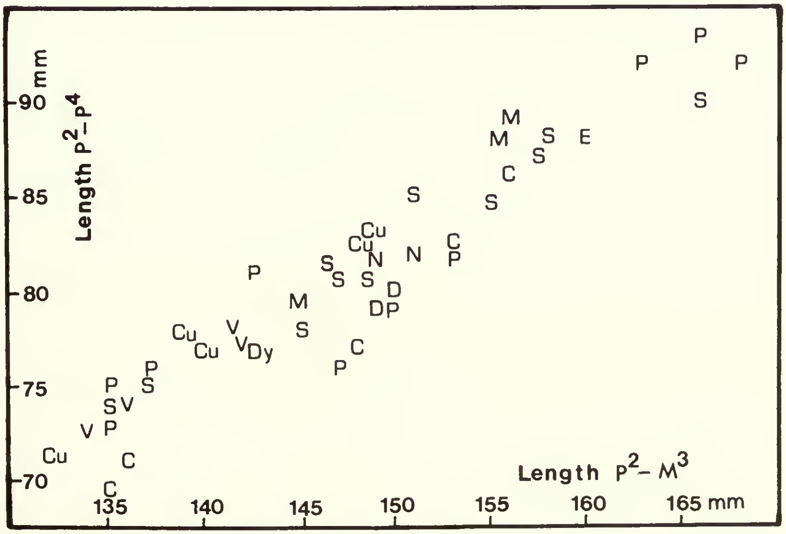

Fig. 6 P^2–P^4 length plotted against P^2–M^3 length. C: Concud, Cu: Cucuron, D: Diavata, Dy: Dytiko, E: Eppelsheim, M: Maraghe, N: Nea Mesimvria, P: Pikermi, S: Samos, V: Vathylakkos.

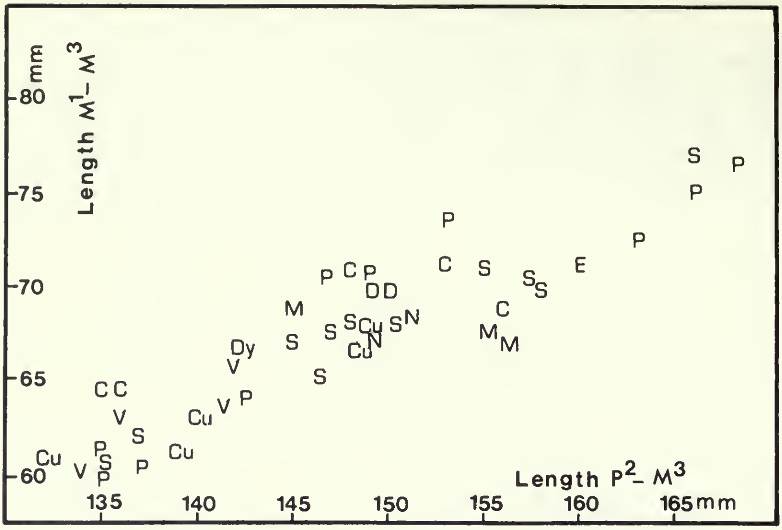

Fig. 7 M^1–M^3 length plotted against P^2–M^3 length. Symbols as in Fig. 6.

M^3: The morphology is comparable to that of the other teeth, but the 'pli caballin' is double or triple and the hypocone is almost round with two well-developed hypoconal grooves. In the left M^3 there is an enamel islet near the 'bouclé prefossette'.

Metrical comparison

A comparison of the present material with that from other localities is given in Figs 6–7. Measurements on teeth of the second and third wear stages were used for all the diagrams because the teeth of the maxillae in the present material are between these stages; the tooth dimensions were measured at the occlusal surface. The length of the tooth series was measured at alveolar level.

In the plots of DAP P^2–M^3 against DAP P^2–P^4 and of DAP P^2–M^3 against DAP M^1–M^3 (Figs 6–7), the Diavata material falls in the middle of the ranges, between the large-sized hipparions (Eppelsheim, large form of Pikermi) and the small ones (Vathylakkos, Dytiko, Cucuron, small form of Pikermi). The Diavata hipparion has an average size similar to the RZO ('Ravin des Zouaves', Axios valley; see p. 342) and Concud hipparions.

Dimensions of individual teeth are compared in Figs 8–11. The material studied is relatively closer to the large and primitive forms of *Hipparion* than to the typical Turolian ones. The tooth dimensions are near those of the hipparions of RZO, Concud and the minimum values of those of Eppelsheim.

Discussion

A well-known Vallesian hipparion is that of Eppelsheim which represents the more primitive form of *Hipparion* (Lower Vallesian). The Eppelsheim hipparion is larger and with more plicated teeth than the Diavata one. Among the Vallesian hipparions there are forms of medium size, with moderate enamel plication and more slender bones than the type of *H. primigenium* (Meyer). Two forms, one of medium size and the other fairly large, are present at the Upper Vallesian locality of Masia del Barbo (Spain), confirming a decrease in the size of *Hipparion* during the Vallesian. A medium-sized hipparion, named *H. depereti* Sondaar, is known from the Upper Vallesian localities of Montredon and Soblay (France). Its teeth

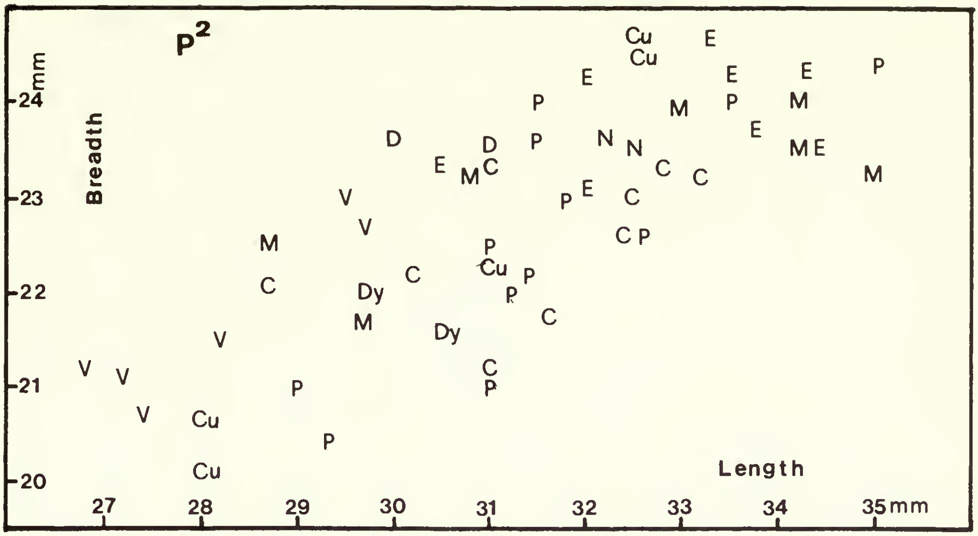

Fig. 8 Tooth breadth plotted against tooth length in P^2. Symbols as in Fig. 6.

are highly plicated, but not so much as in *H. primigenium*, and with ellipitical protocone free from the protoloph, multiplicate 'bouclé prefossette', multiple 'plis caballins', and elliptical hypocone with two hypoconal grooves (Sondaar 1974). All these characters are similar to those of the Diavata material and the dimensions are about the same.

The following Vallesian–Turolian subspecies of *H. primigenium* (Meyer) are known from Spain (Alberdi 1974, Pirlot 1956, Sondaar 1961): *H. p. primigenium, H. p. koenigswaldi*

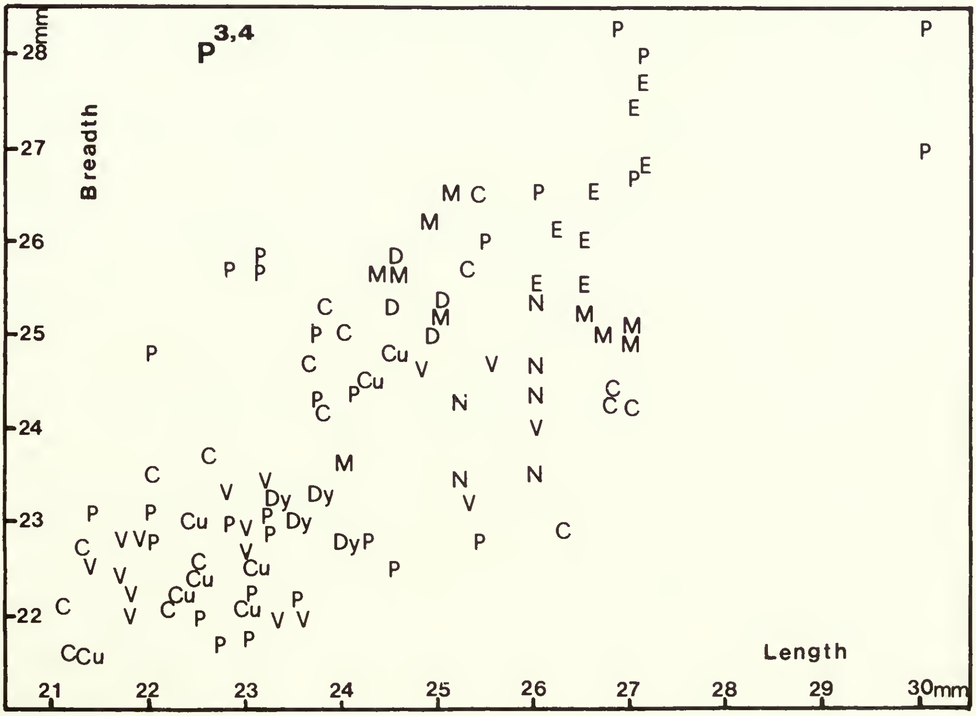

Fig. 9 Tooth breadth plotted against tooth length in $P^{3,4}$. Symbols as in Fig. 6.

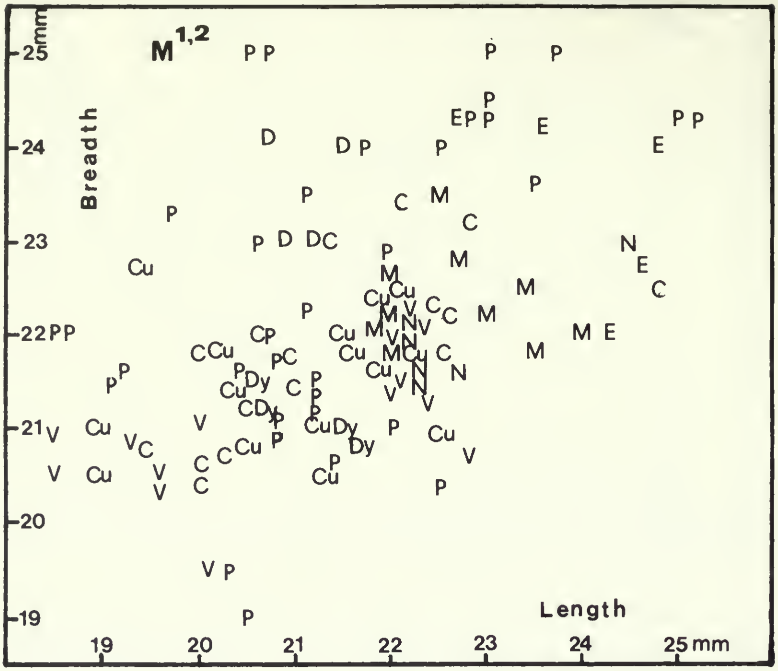

Fig. 10 Tooth breadth plotted against tooth length in $M^{1,2}$. Symbols as in Fig. 6.

Sondaar, *H. p. melendezi* Alberdi, *H. p. catalaunicum* Pirlot and *H. p. truyolsi* Sondaar. All are large forms with highly plicated upper cheek teeth, usually with multiple plis caballins, lingual hypoconal groove and oval unconnected protocone. The Diavata hipparion shows some similarities to *H. p. truyolsi*, such as the triple plis caballins, the slight lingual hypoconal groove, the large protocone and fewer enamel plications than in the typical Vallesian forms. This subspecies represents the transition from Vallesian to Turolian (Alberdi 1974).

Hipparion p. melendezi is also close to the present hipparion especially in features of P^2 morphology, such as the confluent fossettes and the elliptical and connected protocone. It represents the more evolved form of *H. primigenium*, living in the Upper Vallesian (Alberdi 1974). Recently it has been studied again and seems to be closer to *H. concudense* Pirlot and the *Hipparion* sp. from Masia del Barbo than to the Vallesian forms of *H. primigenium* (Forstén 1982).

The other form which is close to the Diavata hipparion is the Upper Vallesian *H. p. catalaunicum* Pirlot. It is like the Diavata hipparion in the form of plis caballins, the slight lingual hypoconal groove and in the dimensions of the tooth series (DAP P^2–M^3 = 149·0 mm; Pirlot 1956).

Thus the Diavata hipparion is closely related to the Upper Vallesian–early Lower Turolian forms, especially to *H. p. truyolsi* Sondaar, a transitional type occurring from Vallesian to Turolian.

Hipparions are known dating from the Upper Vallesian to the end of the Turolian from the lower Axios valley. A maxilla (RZO–1) of a large hipparion is known from the locality 'Ravin des Zouaves', near the village of Nea Mesimvria. This specimen is medium to large in size, and has pronounced enamel plication, a small elliptical or round protocone, double or triple 'plis caballins', multiple 'bouclés prefossettes' and robust metapodials. The RZO hipparion is similar to the Diavata one, but it has a smaller protocone on all the teeth, the lingual hypoconal groove is not very deep and is clearly observed in all the teeth except the

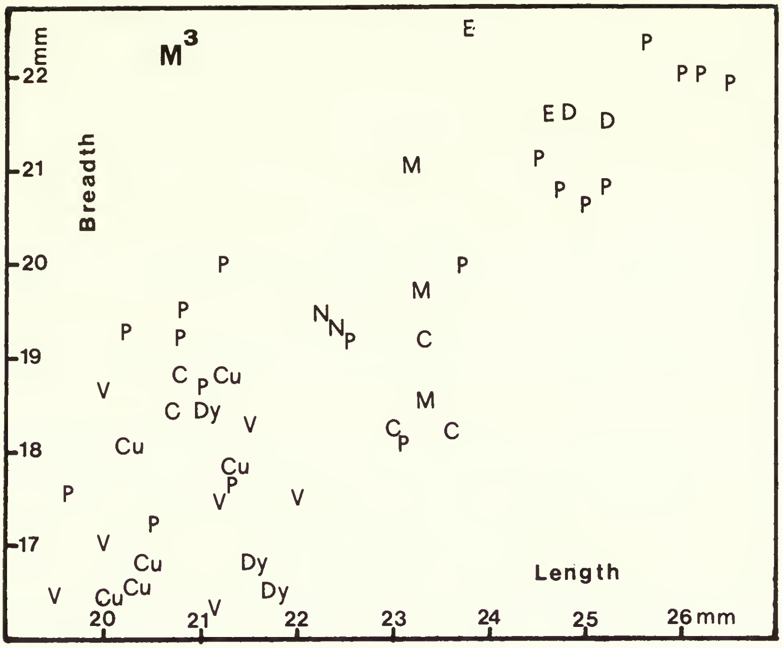

Fig. 11 Tooth breadth plotted against tooth length in M^3. Symbols as in Fig. 6.

M^3, and the 'plis caballins' are less plicated. Another similarity is in the shape of the metacone which is well developed and quadrangular in both specimens. The RZO locality is dated as Upper Vallesian to early Lower Turolian (Koufos 1980).

Two hipparions are known from Pikermi, one large and robust and the other medium-sized and slender. The second form has the characters of the Turolian steppe hipparions, named *H. mediterraneum* (Roth & Wagner). The other has highly plicated cheek teeth, a large subtriangular protocone usually free from the protoloph, two hypoconal grooves and multiple 'bouclés prefossettes'. The Diavata hipparion has smaller dimensions, and less pronounced enamel plication than the large one of Pikermi, which has been named in various ways: *H. brachypus* Hensel (1863), *H. gracile* (Kaup) (Pirlot 1956) and *H. primigenium* (Meyer) (Forstén 1968). The last author noted its relationship to the Eppelsheim hipparion and considered it to represent a Turolian population of *H. primigenium*.

The Turolian hipparions of the lower Axios valley have the characters of the slender, steppe hipparions of this period. They are small to medium-sized with simple to moderately plicated cheek teeth, simple 'bouclé prefossette', usually a small elliptical and isolated protocone, a round and not very large metacone and no lingual hypoconal groove; they thus differ from the Diavata hipparion.

The Diavata hipparion is close in its dimensions to *H. dietrichi* (Wehrli) and *H. proboscideum* Stüder of Samos. The first species is smaller with poor, almost simple, enamel plication, usually a simple 'pli caballin' and an oval protocone which is connected to the protoloph in very worn teeth. The second one is larger with a longer muzzle, moderate enamel plication and a short and wide protocone (Gromova 1952, Sondaar 1971). The Diavata hipparion differs in displaying more primitive characters than the Turolian Samos hipparions.

The above comparisons show that the present species lies between the primitive Vallesian (Eppelsheim) and the more evolved Lower Turolian (Pikermi, Axios valley, Samos) hipparions, with an observable decrease in size and plication number, representing a reduction in primitive characters from the condition at Eppelsheim.

Diagnosis

The characters of the Diavata hipparion can be summarized as follows:

i. medium to large size
ii. pronounced enamel plication in the upper cheek teeth; large subtriangular and isolated protocone (except on the P^2); usually multiple 'plis caballins', and elliptical hypocone with two hypoconal grooves
iii. morphological and metrical similarities to the more primitive hipparions
iv. differences (lower enamel plication, smaller dimensions) from the typical *H. primigenium* of Eppelsheim.

From the discussion above and its characters the Diavata hipparion must belong among the Vallesian forms. We cannot give it a specific name, however, because of the small amount of material, the unknown locality and the large number of described species at this period.

Age of the locality

The material of the Diavata locality consists only of that studied herein, with the addition of the maxilla of the hyaena mentioned above (p. 335). This is of large size, similar to *Hyaena brevirostris* Aymard and *H. gigantea* Schlosser, but because of some differences in the shape of the P^4 it was named *Hyaena salonicae* and dated as Upper Miocene by Andrews (1918). Later the specimen was studied further and was found to be similar to *Crocuta gigantea* (Schlosser), except for the large protocone on the P^4. Pilgrim (1931) considered it to be a different Pontian species of *Crocuta, C. salonicae* (Andrews). In his study of the Pontian hyaenas Kurtén (1957) identified the one from Diavata as in the subgenus *Percrocuta*, and noted that it possibly belongs to the evolutionary line of *C. gigantea, C. carnifex* (Pilgrim) and *C. grandis* Kurtén, but that it is still different enough in the shape of the P^4 and in dimensions to represent a different species, ? *Crocuta* (? *Percrocuta*) *salonicae*. Beaumont (1979) showed that this maxilla is similar to three different species of different ages, and that it could belong either to the Pontian *Adcrocuta eximia* (Roth & Wagner), the Lower Pliocene subgenus *Pachycrocuta*, or the ? Villafranchian *Hyaena* (*Pachycrocuta*) *brevirostris*. The known hyaenas of the lower Axios valley belong to *Adcrocuta*, and although the collected material is sparse the species *A. eximia* is found in the Turolian localities of the area and a new subspecies *A. eximia leptoryncha* Bonis & Koufos has been described from the Upper Vallesian locality of RPl ('Ravin de la Pluie') (Koufos 1980, Bonis & Koufos 1981). But the Diavata hyaena cannot help to determine the age of the hipparion because its systematic position is unknown and its provenance is uncertain.

The age of the Diavata locality can be estimated, however, using the hipparion material itself. There are two *Hipparion* biozones in the Mediterranean Vallesian (Sen *et al.* 1978). The first (Lower Vallesian) is characterized by a heavy hipparion with archaic dental and locomotor characters. The second (Upper Vallesian–early Lower Turolian) has two forms: one medium-sized and heavy and the other an even more robust form; one is smaller, the other larger than the hipparion of the first zone. The primitive characters persist in these hipparions (Sen *et al.* 1978). The Diavata hipparion is morphologically similar to the more evolved Vallesian forms of *Hipparion* and must therefore belong to the second zone of the Mediterranean Neogene, comprising the period Upper Vallesian–early Lower Turolian. A similar age is possible for the giant hyaena if it indeed comes from the same level as the hipparion. A similar age is estimated for this hyaena by Mme Germaine Petter, Musée National d'Histoire Naturelle, Paris (personal communication).

If our continued efforts to find the locality are successful its discovery will help the positive dating of the locality and deposits.

Acknowledgements

I am grateful to Dr A. W. Gentry, who put at my disposal the material, corrected the manuscript and helped me during my visit to the British Museum (Natural History). I thank Mr A. P. Currant who helped me to find Capt. Davies' letter, and also Prof. L. de Bonis and Dr V. Eisenmann for critically reading the manuscript.

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Preparation and further study of the Singa skull from Sudan

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Synopsis

Preparation of the Singa calvaria has permitted study of further morphological and endocranial details. Preparation techniques are described, including the use of acetic acid and ethanolamine thioglycollate, and the specimen was examined for signs of pathology which might account for the unusual cranial shape and diploic thickening. The meningeal vessel patterns and endocast are described, and it is suggested that the Singa individual may have been left-handed. This study provides further data in support of the recent view that the Singa specimen represents an archaic rather than anatomically modern population.

Introduction

The Singa calvaria was discovered in 1924, eroding out of a caliche deposit within the 'Gezira clay' exposed in the west bank of the Blue Nile (Oakley, Campbell & Molleson 1977). Assessments of associated faunal and archaeological materials at Singa and the related site of Abu Hugar have favoured a late Pleistocene age for the specimen (see discussion in Stringer 1979), but recent archaeological work in the area suggests that the skull may have been associated with a Middle Stone Age or even final Acheulian industry, with a probable minimum age of early Upper Pleistocene (Bräuer 1984). The specimen has received comparatively little attention since the first description in 1938 (Woodward 1938) and, as summarized by Stringer (1979), views of its affinities have ranged from workers who classified it as a 'proto-Bushman' (e.g. Woodward 1938) to those who regard it as quite distinct from anatomically modern humans (Brothwell 1974, Stringer 1979). Brothwell (1974) raised the possibility that the unusual cranial shape and proportions of the calvaria were partly pathological in origin, a view supported by Stringer (1979). In the latter paper the hope was expressed that the specimen could be further prepared in order to allow study of endocranial features for the first time, and this has now been achieved.

Preparation of the specimen

When the calvaria was passed to the Palaeontology Laboratory at the British Museum (Natural History), all that was initially required was the removal of approximately 45 g of matrix for dating purposes. In order to obtain this quantity of matrix it was necessary to use a larger opening than that of the foramen magnum. On closer examination of the skull it was seen that at one time most of the occipital region had been broken and then glued back into place. By dissolving the glue and removing the pieces of bone a roughly circular opening about 100 mm in diameter was produced. This opening proved to be an acceptable size through which to work. Once the matrix sample had been removed the next logical step was to take advantage of the situation and prepare the whole of the endocranial surface.

Methods

The first task was in finding a suitable solvent for the glue holding most of the occipital region together. The glued areas were brushed with solvents such as water, industrial

Bull. Br. Mus. nat. Hist. (Geol.) **38** (5): 347–358

Issued 31 January 1985

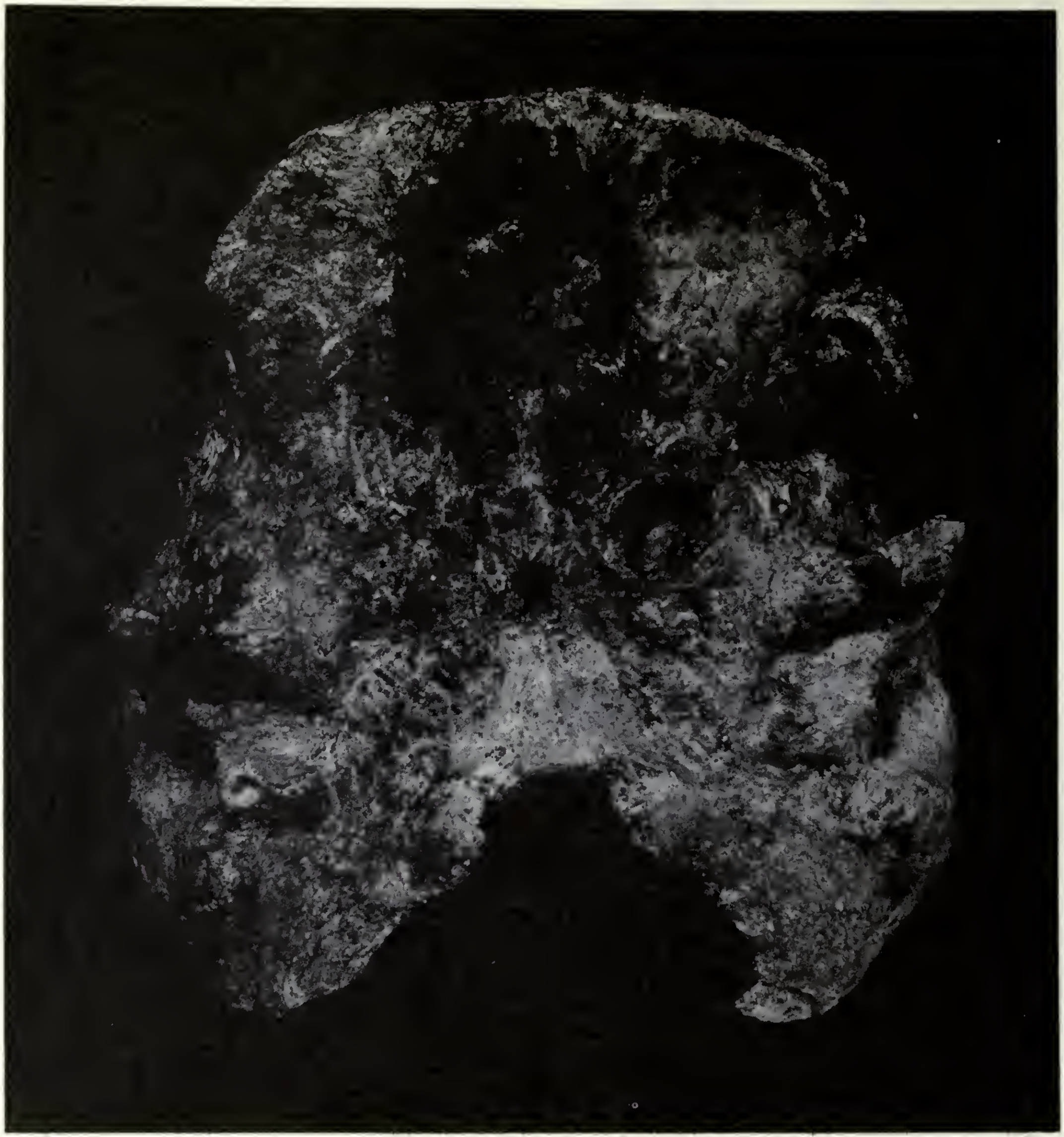

Fig. 1 Inferior view of the Singa cranium before preparation but after removal of rear of vault.

methylated spirit, methyl ethyl ketone and acetone. Only the latter proved to be successful in dissolving the glue and gradually most of the occipital region was successfully detached. These detached pieces were mechanically prepared using a pneumatic engraver, the Desoutter V.P.2, and matrix required for dating purposes was removed using the same tool. Before further treatment was carried out a series of photographs (Figs 1, 3) were taken of the skull for record purposes.

The skull was found in a limestone concretion within the 'Gezira clay' of eastern Sudan (Oakley *et al.* 1977), so it was decided that the safest method of preparation, bearing in mind any fragile structures which could be present, would be to dissolve the limestone matrix chemically, using dilute acetic acid. This organic acid, when used as a dilute aqueous solution, dissolves limestones and breaks down other rocks cemented with carbonates, but it does not react with the phosphatic material constituting the skull (Rixon 1976).

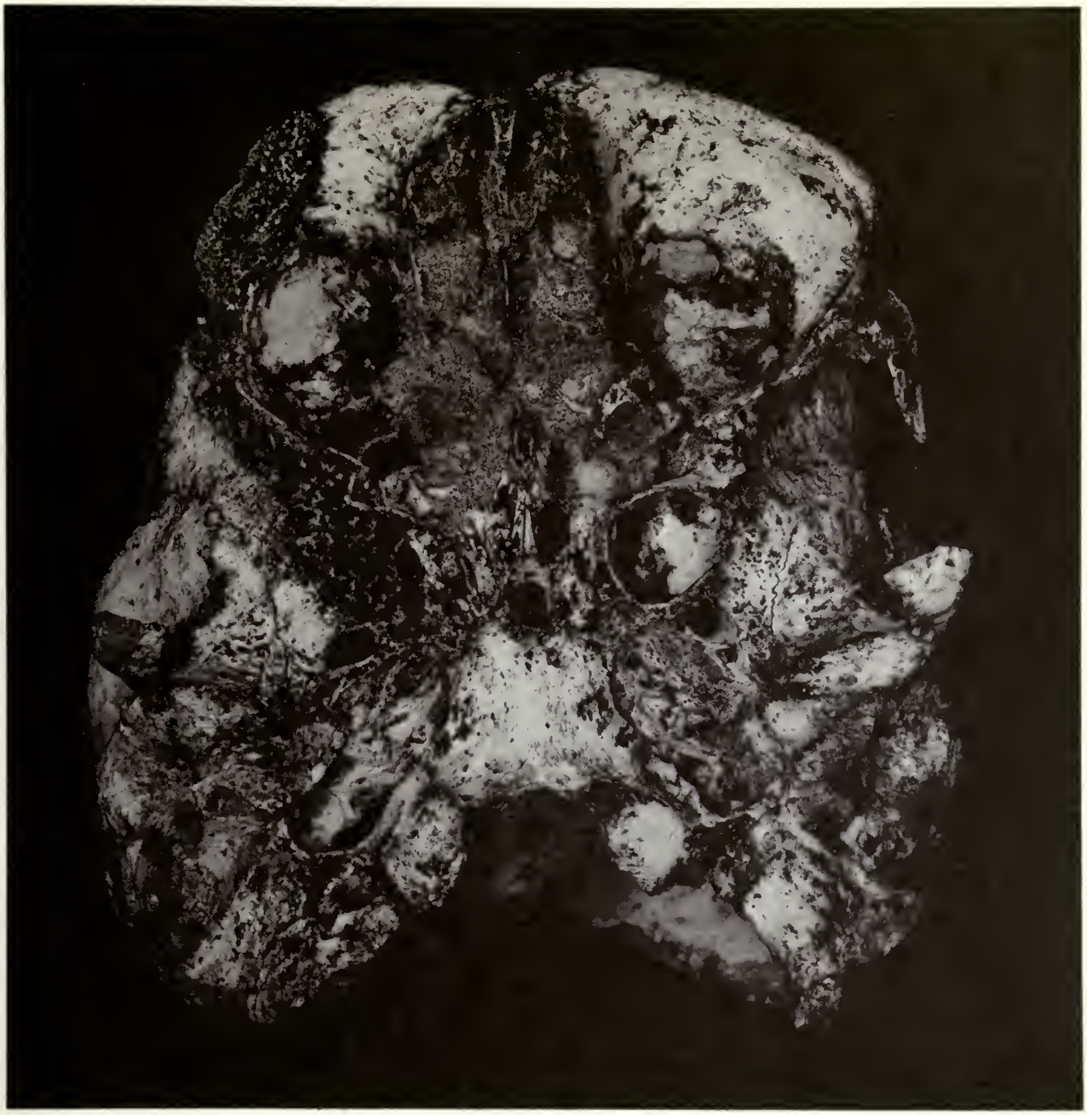

Fig. 2 As Fig. 1, but after final preparation. Note great development of sphenoidal sinus visible through damage on the left side (= right side in this inferior view).

The skull was fully immersed initially in a 1% (v/v) solution of acetic acid in water for about one hour. A low concentration of acid was used in the first instance to gauge the reactivity of the bone and matrix with acid and to provide preliminary cleaning. The skull was then removed from the acid and placed in a small tank with running tap water for 2–3 hours to rinse out the remaining acid and its salts. (Washing time should be at least three times as long as acid immersion time; this is necessary to discourage the growth of calcium acetate crystals during drying, which would disrupt the fossil bone.) During the washing phase, loosened sediment was removed by gently streaming water at the specimen through a pipette. Areas of bone which were too delicate to be cleaned whilst wet were treated after drying in an oven at approximately 50°–60°C for about 24 hours. The whole skull was then cleaned both internally and externally by brushing with methyl ethyl ketone. Exposed bone was then coated with a dilute solution of polybutyl methacrylate (Vinalak 5911) in methyl

ethyl ketone, in the proportion 1:4 v/v. This consolidant was used because of its resistance to acid attack and the fact that it does not swell in water.

When the polybutyl methacrylate solution had dried the skull was immersed in a 3% aqueous solution of acetic acid for about 3 hours and note taken of the extent of reaction. The skull was then washed in running tap water for about 9 hours and subsequently dried in a warm oven as previously described. Any areas of newly exposed bone were cleaned and coated with the polybutyl methacrylate solution. The whole treatment, including 2 hours acid immersion, washing, drying and consolidating was repeated 5 times with a 5% aqueous solution of acetic acid. The acid concentration was increased to speed up the solution of the matrix, but without causing violent effervescence which would have damaged the bone. This concentration of acid was used through the rest of treatment. The immersion time was kept to about 2 hours and washing usually continued overnight.

At this stage of treatment the posterior and anterior clinoid processes were becoming visible and to a slightly smaller extent the lesser wings of the sphenoid bone could be seen.

The grey-brown colour of the bone and red-brown colour of the matrix indicated the probable presence of iron minerals. To help remove these iron minerals and so perhaps aid preparation, a different chemical treatment was tried. This involved immersing the skull in a 5% (v/v) solution of ethanolamine thioglycollate in water for 3–4 hours. The skull was then washed overnight.

Solutions of thioglycollic acid and thioglycollates have been used for derusting iron and steel (Krockow 1966), and have found application in the treatment of fossils for the removal of haematite and limonite matrices (Howie 1974). Ethanolamine thioglycollate, i.e. an aqueous solution of 40% thioglycollic acid containing ethanolamine, will react non-violently with soluble and insoluble iron compounds forming a violet-coloured soluble ferrothioglycollate complex. During immersion of the skull in the ethanolamine thioglycollate solution this violet complex was formed, confirming the presence of iron. After immersion and washing the skull was allowed to dry in air. Short immersion times and thorough washing were imperative to help prevent the violet-coloured complex ferrothioglycollate anion from oxidising to a brown insoluble precipitate which would have covered the skull.

After drying, the skull was examined. The overall colour of exposed bone had changed from grey-brown to off-white, giving the skull a bleached appearance. It was therefore concluded that the original colour was mainly due to the presence of iron compounds. The matrix was also found to be 'crumbly' on the surface and was simply removed by brushing. Later analysis of the matrix for iron, by the atomic absorption method, showed a 1% by weight of iron, present as 1·13% Fe_2O_3 and 0·30% FeO.

The acetic acid treatment was then repeated five times, at which stage the exposed endocranial surface was examined. Cracks had appeared in the fragile posterior clinoid process and a hole had appeared in the posterior fossa leading out through the orbital part of the right frontal bone. A cynoacrylate cement (Powabond 240) was dripped carefully into the smaller cracks and the hole was sealed with an acrylate-based filler, composed of polymethylmethacrylate powder (North Hill Plastic) 4·5 parts (w/w), glass beads (vacu beads) 4·5 parts and sepiolite (magnesium trisilicate) 1 part. Methylmethacrylate monomer (North Hill Plastic) was added to the mixture to initiate curing just before it was used. The glass beads and sepiolite were used in the mixture to counteract shrinkage (Croucher & Woolley 1982). Photographs of the skull were again taken at this stage for record purposes. The skull was then treated a further five times in acid and note was taken between treatments of any changes occurring in the condition of the skull. It was observed that new areas of bone, untreated by ethanolamine thioglycollate but exposed by the acid, were grey in colour. Therefore to a limited extent the progress of matrix removed could be monitored between acid treatments by any increase of the grey areas, indicating newly-exposed bone. The skull was then once more immersed in a 5% solution of ethanolamine thioglycollate, as previously described, to whiten newly-exposed bone.

Areas around the temporal bone proved most difficult to clear, so holes were drilled mechanically from the outside through the matrix in the foramen ovale. A 5% acetic acid

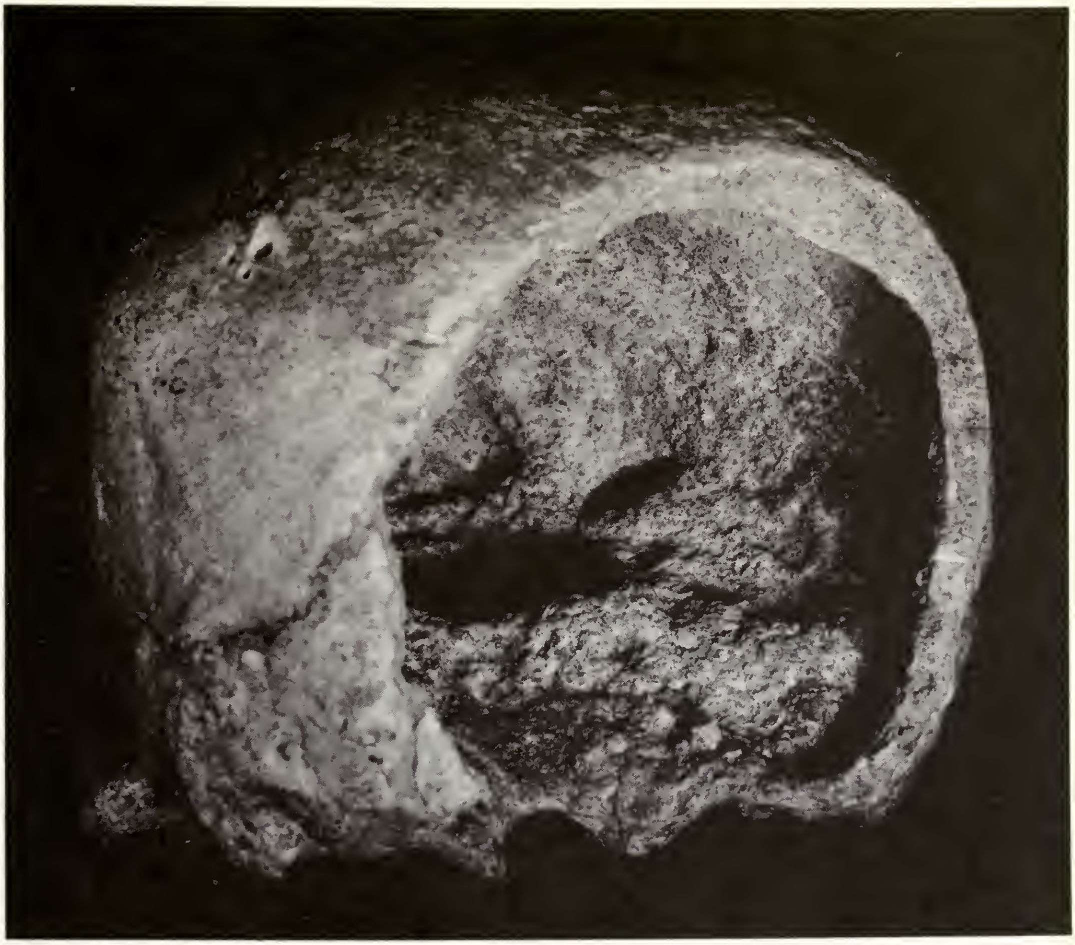

Fig. 3 Posterior view of Singa endocranial surface before preparation.

solution was dripped from inside the cranial cavity and drained to the outside through the drilled holes. This process was carried out for approximately 2 hours, by which time most of the matrix had been removed. The whole skull was then washed for 5–6 hours and allowed to dry. Acid immersion was then carried out twice more, after which it was decided to cease acid preparation. After the second immersion the washing procedure was extended to about 24 hours and the skull was finally washed in deionized water.

On examination of the endocranial surface it was found that most of the matrix had been removed except for a small area on the cribriform plate and near the temporal bone. It was decided that further chemical preparation could bring about damage to the finer structures exposed and also the regions in which matrix remained (mentioned previously) were at an almost impossible angle to prepare mechanically.

Both the internal and external surfaces of the skull were coated with a thin layer of the polybutyl methacrylate solution used previously. A final set of photographs were taken at this stage for record and comparison purposes (Figs 2, 4). The repaired occipital region was then almost fully immersed in a 5% solution of ethanolamine thioglycollate as before to whiten the bone. A small area was intentionally not immersed and marked to indicate that it had undergone no chemical treatment. This area could then be used in future to obtain bone samples for dating. An endocranial cast was made by R. J. Parsons before the repaired, treated occipital region was replaced and cemented with a cynoacrylate cement (Powabond 240).

Palaeopathological aspects

The shape of the Singa skull vault is characterized by an unusual width at the parietal bosses. This increased width is associated with a corresponding increase in the table thickness of the parietal bones (Figs 3–4). Direct measurement of the mid-parietal area at euryon (the points marking the maximum biparietal breadth of the skull) shows a total skull thickness of 14 mm. Is this within the normal range of variation in skull thickness? Measurements on skulls of modern white Americans by Todd (1924) indicate that the average thickness at euryon is 3·56 mm. According to Ethier (1971) some degree of cerebral underdevelopment or a systemic disease, active or healed, should be suspected if the thickest part of the vault exceeds 10 mm. However, some early hominid skulls are known to be considerably thicker than those of modern humans; a thickness of over 10 mm is not unusual (Weidenreich 1943). Certain areas of the skull have also been found to be proportionately thicker than others, particularly the parietal tuberosity in *Homo erectus*. Skulls of Neanderthals are somewhat thinner, but still thicker than the modern average.

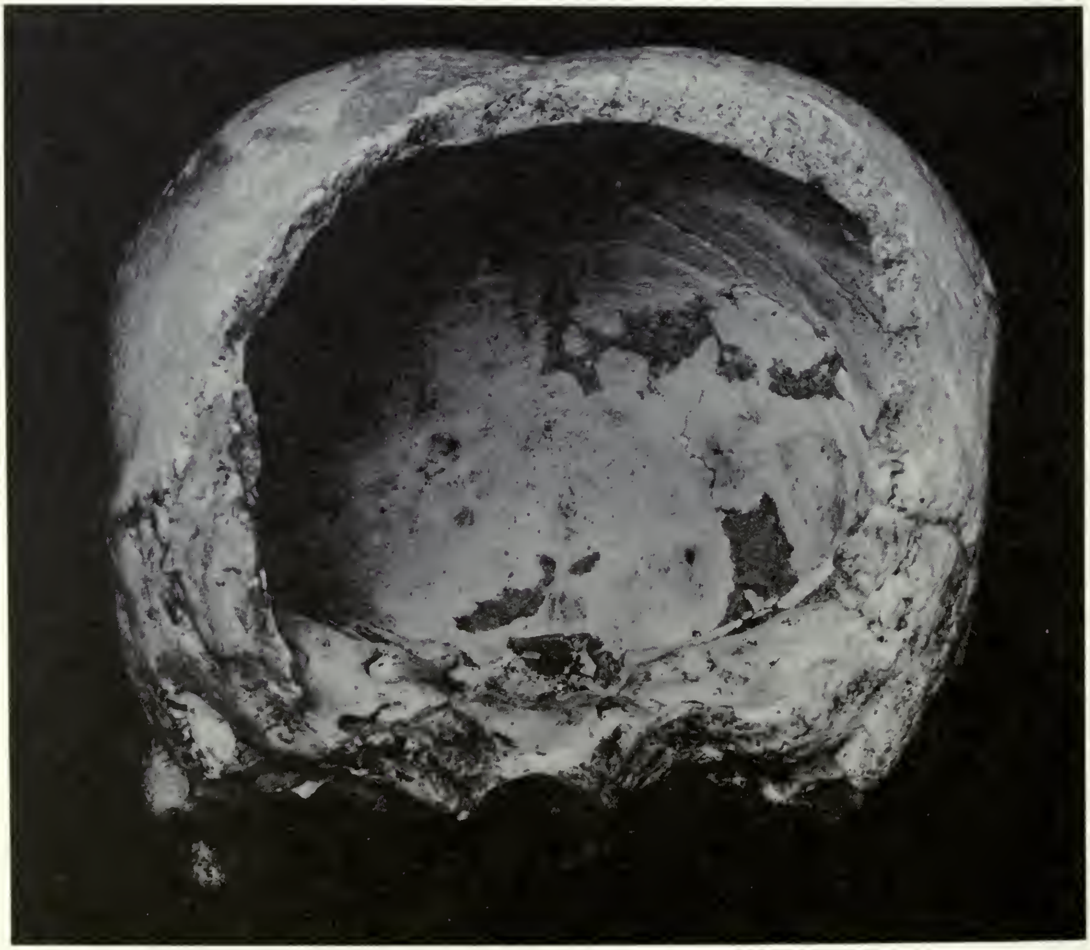

Fig. 4 As Fig. 3, but after final preparation. Note in Figs 3–4 the locally great thickness of the parietal bone revealed by the removal of the rear of the vault along an old fracture line.

If the antiquity of the Singa skull is at least early Upper Pleistocene, then possibly the thickening in the parietal region is not outside the normal range of variation of hominids at that time. The vault thickness of the specimen is generally marked, ranging from 7 mm on the parietals and occipital near asterion to 15 mm at inion. Thickness at the midfrontal, bregma and lambda is *c.* 9 mm, and therefore midsagittal vault thickness is certainly high compared with many Neanderthals. Moreover the thickness at the parietal tuberosity on each side is outside the Neanderthal range and is matched only by the thickest *H. erectus* crania. However, total skull thickness by itself is a poor criterion for assessing the presence or absence of pathological change. Any number of factors including age, sex and individual variation can have an effect on total skull thickness. Normal skulls may be either 'diploic' with a prominent middle table or 'compact' with very little diploic bone (Ethier 1971). In either case the ratio of compact to diploic bone remains about the same; that is a diploic skull will have a correspondingly thicker layer of compact bone. The thickness of the normal skull will always be proportionate to the width of the middle table. Alterations in the normal ratio of compact to diploic bone are a much more significant sign of pathological change.

Weidenreich (1943) did not find an abnormal ratio of compact to diploic bone associated with skull thickening in early hominid material. He found that all three tables of the skull vault were almost equally involved in the thickening, with the inner and outer table contributing slightly more to the overall thickness than the diploe. This is not the case with the Singa skull; the diploe contributes much more to overall thickness than the compact bone. Measurements of the parietal bone show the ratio of compact to diploic bone to be 1:3·9. Data from modern individuals show that the normal ratio of compact to diploic bone in the parietal area averages 1:1·4 (Reynolds 1962). The diploic width of normal individuals was considered to be less than 2·3 times the combined width of the inner and outer table (Reynolds 1962, Sebes & Diggs 1979). The diploic bone in the parietal area of the Singa skull is almost four times the width of the compact bone, which is outside the normal range in modern individuals, and is quite unlike the pattern found in earlier hominids.

Hyperostotic changes of the middle table of bone are usually manifestations of metabolic or developmental diseases (Ethier 1971), Anaemias, in particular, are known to be the most common cause of an increase in the middle table of bone. Anaemias are also known to be associated with changes in vault shape similar to that seen in the Singa skull. As a result it was decided to test the hypothesis that the vault shape and diploic thickening seen in the Singa skull are the result of an anaemia.

On the basis of observations of clinical radiographs of patients with anaemia several criteria have been developed for comparative use with anthropological material (Stuart-Macadam 1982). These criteria represent changes which develop because of the body's basic adaptive mechanism to anaemia: an increase in bone marrow cells. A great increase in the red marrow can produce pressures on the adjacent bone which result in many of the bone changes associated with anaemia. Taken individually, the criteria may occasionally be present on radiographs of normal skulls, but as a group they illustrate a pattern of bone change seen in anaemias with erythrocytic hyperplasia. The seven criteria are:

(1). 'Hair-on-end' trabeculation: the normal circumferentially laid down bony trabeculae radiate out at a 90° angle to the bony tables. This appearance has been found in approximately 5–10% of clinical cases of anaemia.

(2). Thinning of the outer table: the pressure of the expanding marrow can cause a thinning or even disappearance of the outer layer of compact bone as seen on a radiograph. In clinical cases this change has been found in 20% to over 90% of patients with severe anaemia.

(3). Texture changes. Instead of the normal homogeneous pattern of trabeculae seen on a skull radiograph, a coarse, granular pattern with an increase in radiolucency can occur. In clinical studies this has been noted in 25–50% of skull radiographs of patients with various anaemias.

(4). Diploic thickening: this has often been noted in cases of anaemia but has rarely been quantitatively assessed. The diploe has been considered to be abnormally thickened if it exceeds 2·3 times the combined width of the inner and outer tables of bone.

(5). Orbital roof thickening: this is apparent on examination of the orbital roof on lateral radiographs. It has not been quantitatively assessed in clinical studies but is not an unusual occurrence in cases of anaemia. A thickness of over 3 mm is considered to represent abnormal thickening of the roof (Stuart-Macadam 1982).

(6). Orbital rim changes. Normally the orbital rim on a posterior–anterior skull radiograph shows as a distinct, continuous radiopaque curved line. Although it has not been noted in clinical studies, observations of radiographs of patients with severe anaemia show that the rim can develop an increase in radiolucency and appear thinned, flattened or even obscured (Stuart-Macadam 1982).

(7). Sinus height. Clinical studies have shown that in some case of anaemia, marrow overgrowth can retard or even completely inhibit normal sinus development (Caffey 1978, Reimann *et al.* 1975). In these cases, reduction in normal frontal sinus height or even a total lack of development can occur.

Posterior–anterior and lateral radiographs of the Singa skull were taken (125 kV, 160 mA for 2·5 seconds, using Agfa Gevaert Structurix film which was manually processed; focus to film distance 91 cm). Observations showed that with the exception of the diploic thickening of the parietals, the Singa skull did not exhibit any of the other radiographic criteria associated with bone changes in anaemia. There was also no sign of porotic hyperostosis; these porotic lesions of the orbit and skull vault are commonly accepted as osteological evidence for anaemia. On the basis of these results there is little to support the hypothesis that anaemia was responsible for the unusual shape and diploic thickening seen in the Singa skull. It could even be argued that these features are within the normal range of variability expected for the whole population. However, we feel that the cranial shape, abnormally short parietal length, diploic thickening and extensive sphenoidal sinus development are unusual features both for archaic and modern Upper Pleistocene hominids, and deserve further investigation.

Morphological features of the calvaria

Preparation of the specimen has revealed new external and internal details. The robusticity of the temporal bone in the area of the root of the zygomatic process can be seen more clearly, but further study suggests that the reported prominence of the occipitomastoid crest (Stringer 1979) is more a reflection of the small size of the mastoid process than a significant morphological feature. One of the most notable features of the prepared base is the marked development of the sphenoidal sinus (Figs 1–2). Preparation of the specimen has also allowed clearer radiographs to be obtained and these show a fairly large frontal sinus as well, consisting of two simple lobes on each side, the most lateral extending to above the mid-orbit. The occipital bone can now be seen to show a typically 'modern' pattern of venous sinus drainage, and endinion is positioned close to external inion.

Endocranial morphology

The endocranial surface is well preserved, and allowed the preparation by R. J. Parsons of an endocranial cast of silicone rubber with plaster internal support (Figs 5–6). Three determinations of endocranial volume by water displacement each gave values of 1340 ml, which compares closely with a determination by millet seed of 1335 ml. These figures are lower than those estimated previously by calculation or partial endocranial volume determinations (Stringer 1979). While the newly-determined endocranial volume of Singa is typical of modern values, it is low compared with means of Upper Pleistocene samples such as the European Neanderthals (1510 ± 150 ml, N = 6), the Skhūl-Qafzeh hominids (1545 ± 27 ml, N = 5) or European early Upper Palaeolithic hominids (1577 ± 135 ml,

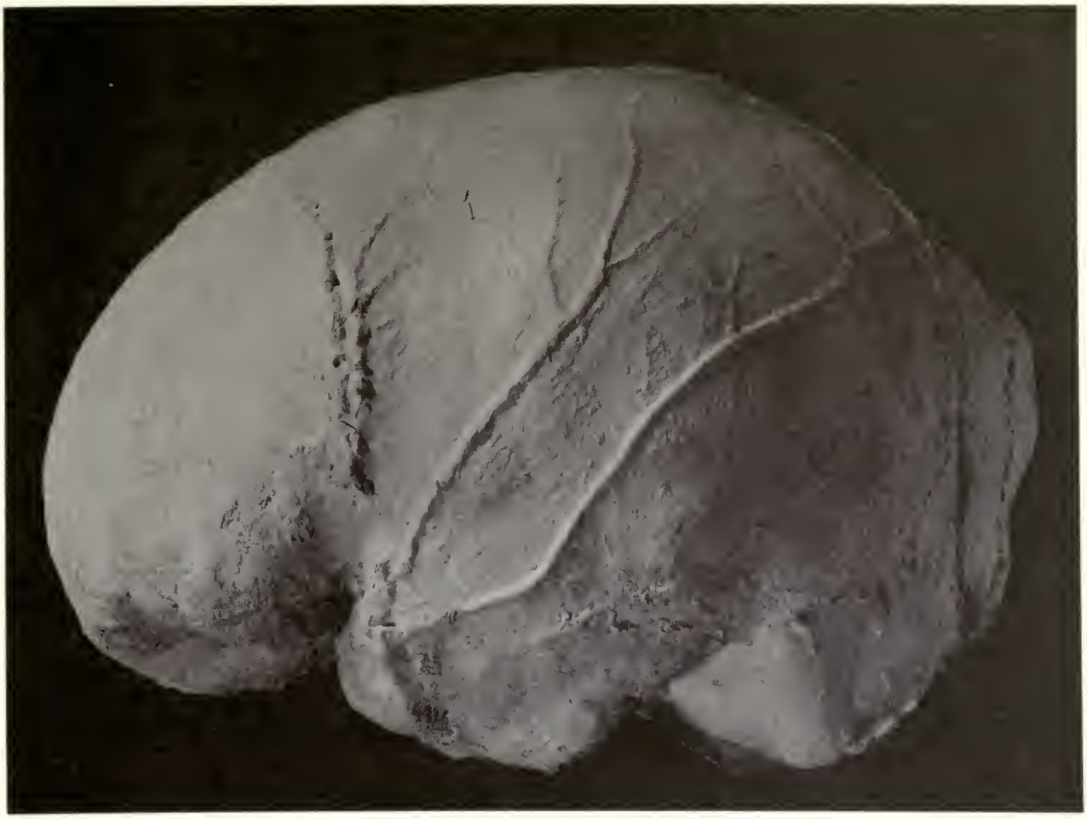

Fig. 5 Left lateral view of endocranial cast, × 0·83.

N = 11) (data from Trinkaus, 1983). However, the Singa value is larger than those obtained for hominids such as Djebel Irhoud 1 (1305 ml, Holloway 1981*b*) or a Ngandong sample (1151 ± 99 ml, N = 5, Holloway 1980).

The endocranial mould preserves little sulcal or gyral relief, but the meningeal vessel patterns on both sides are clear, relatively simple, and asymmetrical. On the left side (Fig. 5) there is a strong anterior (bregmatic) branch which follows the course of the coronal suture,

Table 1 Endocast indices; comparative data from Holloway (1980, 1981*a*, *b*).

(Sample)	*Australopithecus* (4)	*H. erectus* Java (6)	Ngandong (5)	Spy 1 (1)	Spy 2 (1)	Irhoud 1 (1)	Singa (1)	Modern (4)
Breadth/length	0·78	0·79	0·77	0·82	0·78	0·82	0·85	0·78
Breadth/height	1·13	1·28	1·25	1·24	1·20	1·29	1·31	1·08
Length/height	1·44	1·62	1·61	1·52	1·54	1·58	1·54	1·40
Bregma–lambda arc/chord	1·08	1·04	–	1·05	–	1·05	1·08	1·09
Bregma–asterion arc/chord	1·18	1·20	–	1·24	–	1·23	1·25	1·23
Height^3/volume	1·24	0·97	0·98	1·20	0·93	0·99	0·94	1·25
Breadth arc/chord	1·55	1·60	–	–	–	–	1·58	1·72

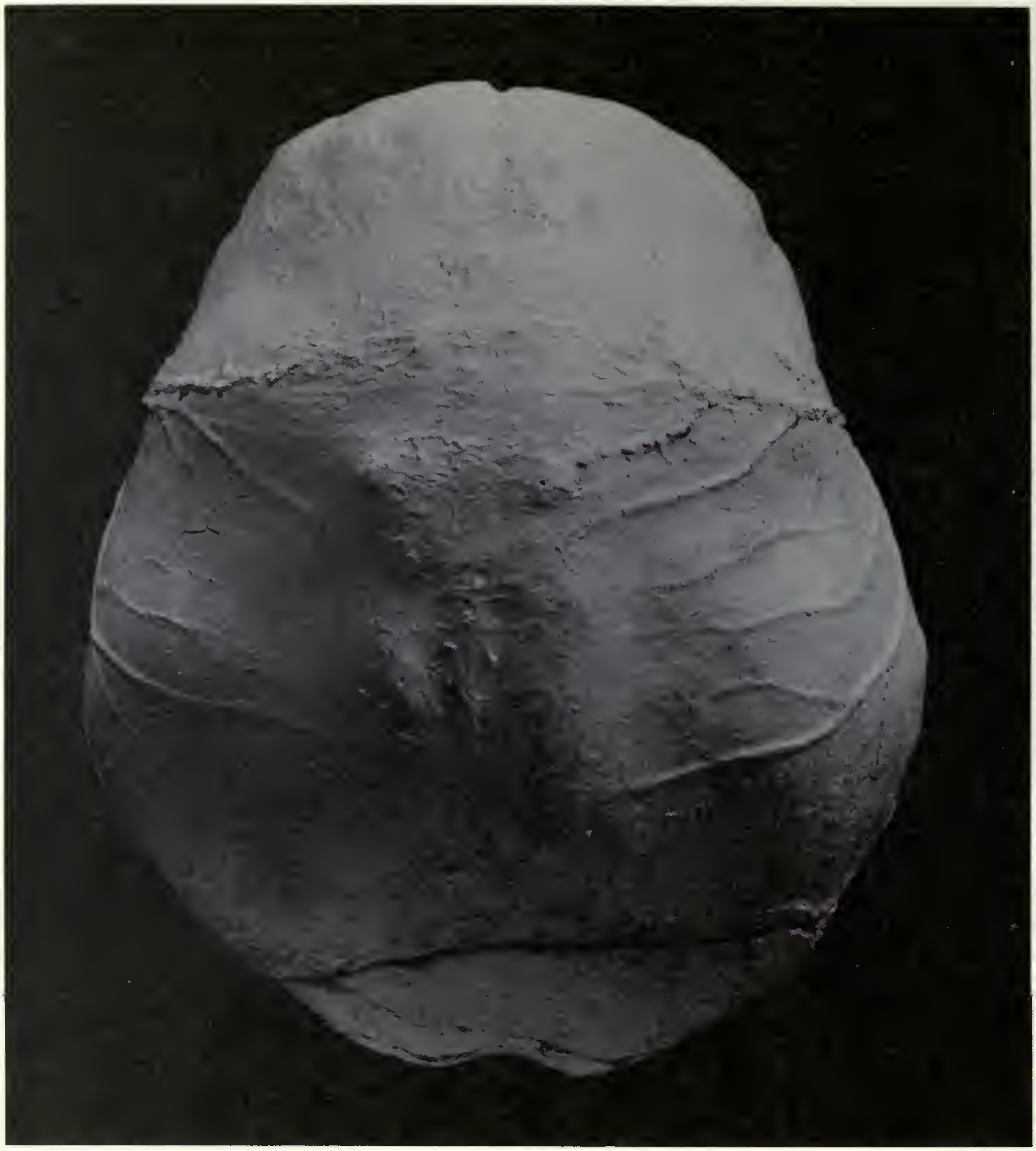

Fig. 6 Superior view of endocranial cast, ×0·83, showing unusual left frontal–right occipital petalial pattern, perhaps indicative of left-handedness.

and well-developed middle and posterior branches which originate virtually together above the temporal lobe. On the right side there is again a strong vertically orientated anterior branch, but posteriorly there is only a single branch originating above the main development of the lateral sulcus. This branch crosses the mid-parietal area and gives rise to a subsidiary superior branch after about 15 mm. The posterior part of the parietal appears to have been drained by a separate and inferiorly placed vessel which runs across the posterior part of the temporal lobe.

In general dimensions the Singa endocast is short (frontal–occipital poles, 166 mm, left and right sides), moderately flattened sagitally (dorsal arc, 233 mm both sides), very broad and flattened (biasterionic breadth 111 mm, temporal breadth 141 mm, arc 223 mm), and rather low (height 108 m). Additional dimensions measured are bregma–lambda chord and arc, 89·5 and 96·5 mm, and bregma–asterion chord and arc 126 and 158 mm (left side), and 128 and 160 mm (right side).

The proportions of the endocast are more similar to those of non-modern hominids, even including *H. erectus* specimens, than to those of a small modern sample measured by Holloway (Table 1). It is particularly in indices reflecting the relative breadth of the endocranial cast that the Singa specimen appears distinct from the modern endocasts, and assuming that pathological aspects have not played a major part in determining endocranial proportions, this provides further evidence that the Singa calvaria may not represent an anatomically modern specimen (Brothwell 1974, Stringer 1979).

The endocast also shows some interesting structural asymmetry. As discussed in Galaburda *et al.* (1978) and Holloway (1980, 1981*a*, *b*), human endocranial surfaces tend to show a characteristic asymmetrical development of localized depressions (petalia) which can generally be related to handedness in living individuals. The characteristic petalial pattern for right-handed individuals is that they show left occipital and right frontal petalias, related to the larger volume of the equivalent brain lobes. Holloway has recognized this same combination of features in various fossil hominid endocasts representing *H. erectus*, Ngandong, Djebel Irhoud, Salé and Neanderthal individuals. However, the Singa endocast shows a clear right-occipital, left-frontal petalial pattern, whether viewed superiorly (Fig. 6) or inferiorly. This unusual morphology may indicate that the Singa individual was left-handed.

Concluding remarks

Preparation of the Singa calvaria has allowed study of certain morphological and endocranial details for the first time. While a specific pathological disorder has not been identified, it is still suspected that the diploic thickening at the parietal bosses and perhaps also the sphenoidal sinus development and certain cranial and endocranial characteristics may be due to a pathological cause. The robusticity of the specimen, the simplicity of the meningeal vessel patterns, and the endocranial proportions all support the view that the Singa calvaria represents an archaic rather than a more recent human population.

Acknowledgements

We would like to thank P. J. Whybrow and R. Croucher for advice during the preparation of the specimen in the Palaeontology Laboratory, BM(NH), R. J. Parsons for the preparation of the endocast, G. du Boulay and O. Wilson (Nuffield Institute of Comparative Medicine) and T. I. Molleson for radiographic work and advice, and the Photographic Unit of the BM(NH) for Figs 1–6.

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Carboniferous and Permian species of the cyclostome bryozoan *Corynotrypa* Bassler, 1911 and their clonal propagation

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Synopsis

Two rare cyclostome bryozoans are redescribed: *Corynotrypa thomasi* Condra & Elias from the L. Carboniferous of Alabama and U. Carboniferous of Nebraska, and *C. voigtiana* (King) from the U. Permian of Durham and Thuringia. Colonies consist of adnate, uniserial branches of simple, elongate-pyriform zooids. Lateral branches arise sporadically as distolateral buds. Colony growth commences from groups of 2–4 radiating zooids united at their narrow proximal ends. None of these zooids possesses a protoecium diagnostic of an ancestrula, and indications of damage suggest that these colony origins may be the products of fragmentation and regeneration rather than of larval settlement. The occurrence of clones of colonies (ramets) arising from fragmentation may have been common in *Corynotrypa*. Preliminary morphological evidence indicates that late Palaeozoic corynotrypids may be less closely related to primitive post-Palaeozoic cyclostomes than are some early Palaeozoic crownoporids.

Introduction

One of the outstanding current problems in bryozoan evolution concerns the phylogenetic relationships between Palaeozoic and post-Palaeozoic stenolaemates. A widely held view is that the dominant Palaeozoic stenolaemate orders (Trepostomata, Cryptostomata, Fenestrata, Cystoporata) became extinct at the end of the Permian, and that all post-Palaeozoic stenolaemates are cyclostomes, descended from Palaeozoic cyclostomes, a comparatively minor group until the Jurassic. This view is now known to be incorrect in at least one respect; unequivocal trepostomes survived the Permo–Triassic extinction event and are found in Triassic deposits from various parts of the world (e.g. Fritz 1961, Morozova 1969, Smit 1976, Sakagami & Sakai 1979). In addition, morphological similarities between various groups of post-Palaeozoic cyclostomes and Palaeozoic trepostomes, cryptostomes and cystoporates, previously attributed to convergent evolution, are reinterpreted by Boardman (1981, 1984) as probable indicators of phylogenetic affinity. If any of these interpretations are correct then post-Palaeozoic cyclostomes are polyphyletic, descended in part from Palaeozoic trepostomes, cryptostomes, cystoporates and cyclostomes.

Cyclostomes of late Palaeozoic age clearly have an important bearing on the ancestry of post-Palaeozoic cyclostomes. However, the late Palaeozoic record of cyclostomes is unfortunately very meagre. Excluding hederellids, which are of doubtful bryozoan affinity (Brood 1975), the only late Palaeozoic cyclostomes thus far described are a few corynotrypids. These include Devonian species of *Corynotrypa* from Canada, France and Poland described by Bassler (1911) and Kiepura (1973), and Devonian to Permian species of the erect genus *Lagenosypho* from several parts of the world described by Langer (1980). Only two post-Devonian species of *Corynotrypa* are known, *C. thomasi* Condra & Elias from the Carboniferous of the USA, and *C. voigtiana* (King) from the Permian of Britain and Germany. The purpose of this paper is to redescribe these two rare species based on a study of type specimens, and augmented by some new material of superior preservation. Particular attention is focused on colony propagation in these and other species of *Corynotrypa*.

Bull. Br. Mus. nat. Hist. (Geol.) **38** (5): 359–372

Issued 31 January 1985

Abbreviations of specimen repositories are as follows: British Museum (Natural History), BMNH; Nebraska Geological Survey (University of Nebraska State Museum, Lincoln), NGS; University College Galway, UCG; Naturwissenschaftliches Museum Coburg, NMC.

Systematic descriptions

Order **CYCLOSTOMATA** Busk, 1852

Suborder **PALEOTUBULOPORINA** Brood, 1973

Family **CORYNOTRYPIDAE** Dzik, 1981

Genus ***CORYNOTRYPA*** Bassler, 1911

TYPE SPECIES. *Hippothoa delicatula* James 1878. Middle Ordovician of N. America and Esthonia, U. Ordovician of N. America (Bassler 1911).

REMARKS. *Corynotrypa* has encrusting colonies composed of uniserial branches of simple zooids, narrow proximally but broadening distally, terminated by a circular or subcircular aperture sometimes with a slight peristome. Unlike most other uniserial cyclostomes, *Corynotrypa* lacks calcified interior walls and the chambers of successive zooids are in spatial continuity via the pore-like structure formed by the narrow proximal parts of the zooids (Boardman & Cheetham 1973, Brood 1975).

Bassler (1911) recognized three subdivisions of *Corynotrypa* according to the shape of the zooecia: a *C. delicatula* subdivision with zooecia narrow throughout their lengths, a *C. inflata* subdivision with zooecia initially very narrow but becoming bulbous distally, and a *C. dissimilis* subdivision with zooecia moderately broad throughout their lengths. However, Bassler acknowledged the existence of intermediate morphologies and the two species described herein lie somewhere between the *C. delicatula* and *C. dissimilis* subdivisions.

RANGE. Middle Ordovician–Upper Permian. The only two post–Palaeozoic records of *Corynotrypa* cited by Bassler (1911) are erroneous; *C. smithii* (Phillips) from the Middle Jurassic of Yorkshire is a bioimmured ctenostome assigned to *Arachnidium* by Taylor (1978), and *C. tenuichorda* (Ulrich & Bassler) from the Palaeocene of Virginia was later reassigned to the cheilostome genus *Hippothoa* by Canu & Bassler (1933: 71).

Corynotrypa thomasi Condra & Elias 1944

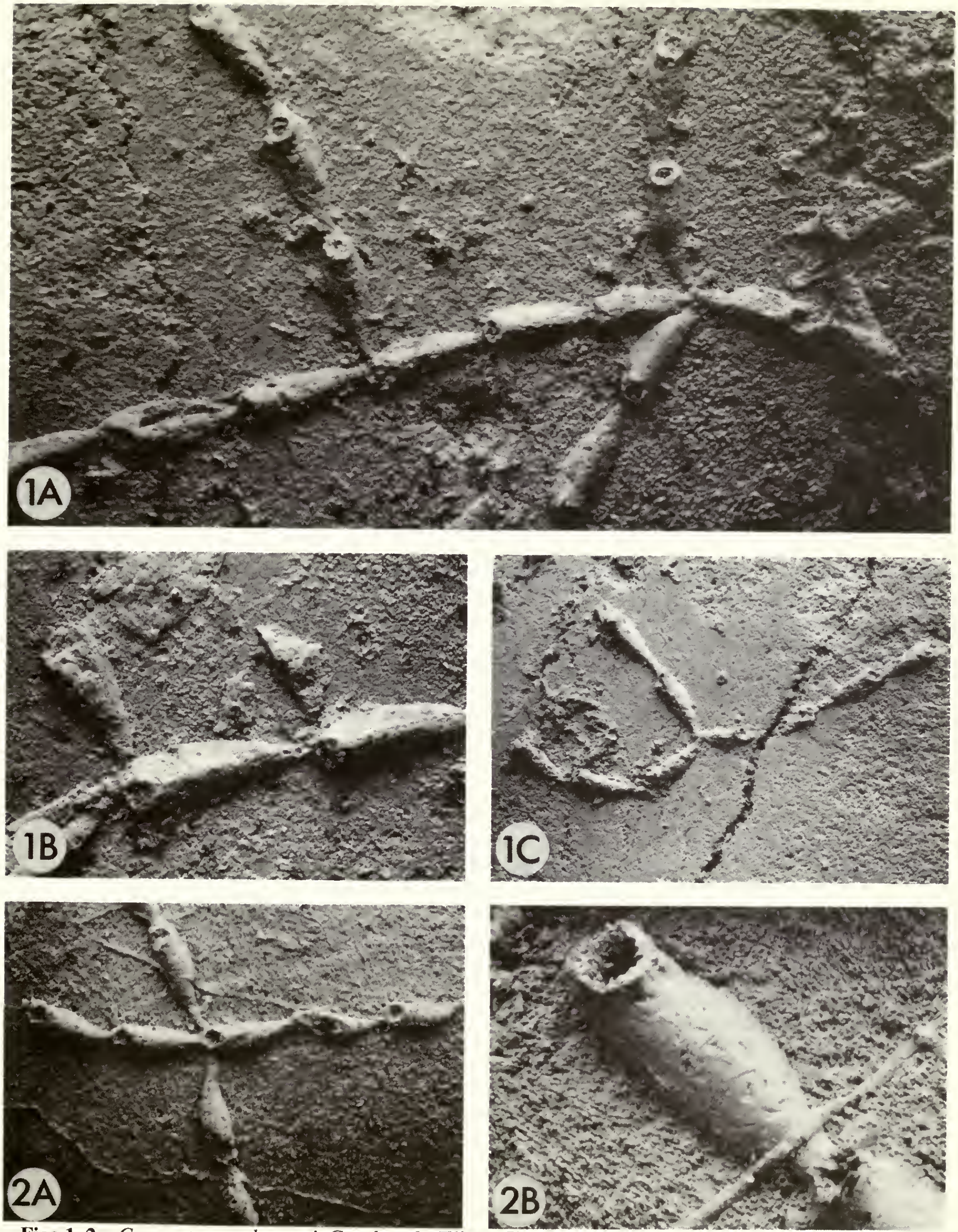
1944 *Corynotrypa thomasi* Condra & Elias: 538; pl. 91, figs 1–4.

HOLOTYPE. NGS 256. Spring Branch Limestone Member, Lecompton Formation, Shawnee Group, Pennsylvanian (U. Carboniferous). Snyderville Quarry, 3 miles west and 1 mile north of Nehawka, Nebraska, U.S.A. Encrusting the interior of a valve of *Pinna peracuta* (*fide* Condra & Elias 1944).

OTHER MATERIAL. BMNH PD6023, PD6216, Bangor Limestone (lower), Chesterian, Mississippian (L. Carboniferous). Fox Trap (Sec. 31, T5S, R10W), Old Bethel Quadrangle, Colbert County, Alabama, U.S.A. (see Thomas, Mack & Waters 1980 for locality details). PD6023 encrusts the brachiopod *Coelidium explanatum* and was collected by P. D. Taylor during October 1982; PD6216 encrusts a bellerophontid collected by F. K. McKinney.

Condra & Elias (1944) mention two specimens additional to their holotype. NGS 257 from the type locality is missing (R. K. Pabian *in litt.*, May 1983). A specimen thought to be NGS 258, from the Dover Limestone (Wabaunsee Series, Pennsylvania) of Pawnee City, Nebraska, no longer bears any trace of the *C. thomasi* colony that was figured by Condra & Elias (1944: pl. 91, figs 3–4).

DESCRIPTION. Colonies are entirely encrusting and consist of branches of uniserially-arranged zooids sparsely covering the substratum (Fig. 1A). Colony branches tend to be gently curved



Figs 1–2 *Corynotrypa thomasi* Condra & Elias. Fig. 1, NGS 256; Spring Branch Limestone Member, Lecompton Formation, Shawnee Group, Pennsylvanian (U. Carboniferous); Snyderville Quarry, Nehawka, Nebraska, U.S.A. 1A, part of large colony, × 35; 1B, two daughter branches forming as distolateral buds, × 50; 1C, small colony on same substrate, × 20. Fig. 2, BMNH PD6023; Bangor Limestone (lower), Chesterian, Mississippian (L. Carboniferous); Fox Trap, Colbert County, Alabama, U.S.A. 2A, paired lateral daughter branches, × 25; 2B, well-preserved zooid lacking pseudopores and crossed by the thread of a vinellid, × 95.

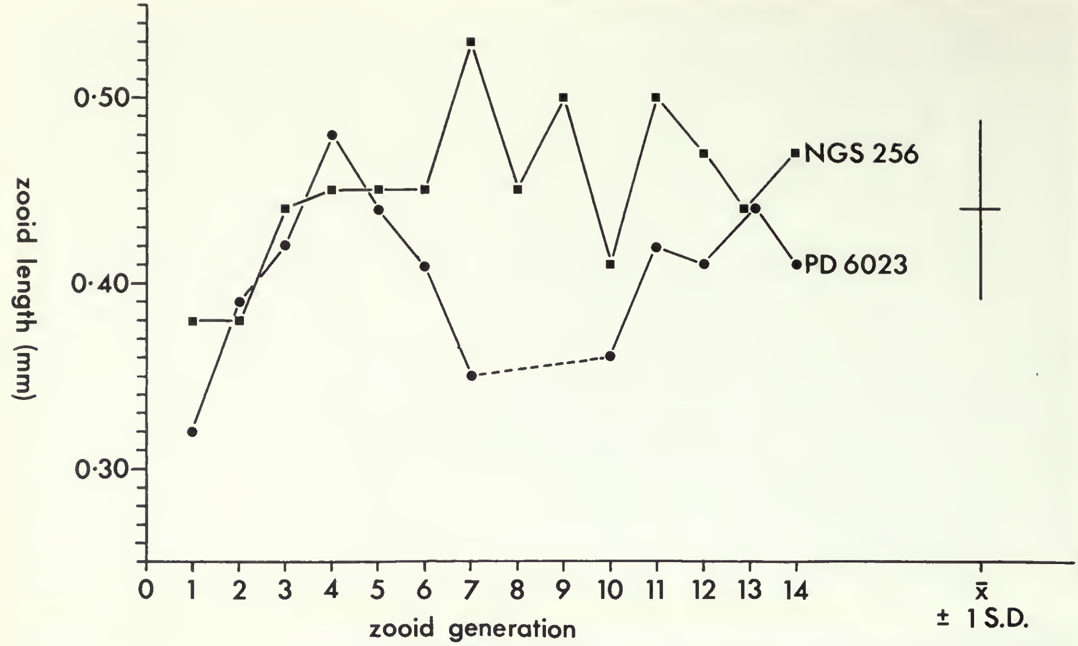


Fig. 3 Astogenetic variation in zooid length in colonies of *Corynotrypa thomasi* Condra & Elias from the U. Carboniferous of Nebraska (NGS 256) and L. Carboniferous of Alabama (BMNH PD6023). Successive zooids were measured outwards from the smallest zooids present in the apparent colony origins shown in Figs 6A and 7A. A slight gradient of astogenetic change seems to be present in both colonies. The bar at the right of the figure indicates the mean value and standard deviation calculated from 102 measurements of zooid length in *C. thomasi* (Table 1).

owing to a combination of the slightly curved shape of many zooids and non-alignment of the longitudinal axes of successive zooids. Division of branches is infrequent and lacks any obvious regularity of pattern. Daughter branches are lateral branches arising from the distolateral budding of a new zooid from a zooid on the parent branch (Fig. 1B). Fifteen per cent or fewer of zooids in each colony give rise to such a distolateral bud, which are usually single but occasionally paired, one either side of the zooid (Fig. 2A). Lateral branches diverge from the parent branch at about 60°–90°. Few branch intersections are observed and the result of intersections are variable; overgrowth of the earlier-formed branch followed an intersection in NGS 256, whereas cessation of growth was the apparent outcome of an intersection in BMNH PD6023 (cf. Gardiner & Taylor 1982). Branches may be traced proximally to a colony origin (Figs 6, 7), consisting of a group of two to four radiating zooids joined at their proximal ends (see below, p. 367).

Zooids are small and elongate pyriform in shape, narrow proximally and broadening distally to attain their maximum width at about two-thirds the length of the zooid. Well-preserved frontal walls are smooth and lack pseudopores (Fig. 2B); weathered frontal walls have a microstructural fabric parallel to the length of the zooid. The terminal aperture is circular or subcircular and small (*c.* 0·07 mm in diameter). Peristomes are rarely preserved and when present (e.g. in a hollow on the substratum of BMNH PD6023) they are slight and inclined somewhat distally. A poorly-defined zone of modest astogenetic change in zooid length may occur outwards from the early stages of growth (Fig. 3). In BMNH PD6023, but not in NGS 256, the first zooid in each daughter branch is longer than usual, averaging 0·54 mm, compared to 0·44 mm for zooids in the colony as a whole.

Table 1 Zooid dimensions in *Corynotrypa thomasi* Condra & Elias, and *C. voigtiana* (King). Abbreviations: $\bar{x}$ = mean value (mm); SD = standard deviation (mm); CV = coefficient of variation; r = observed range (mm); Nc = number of colonies (*either 2 or 5 colonies of *C. thomasi* were measured depending on whether the holotype specimen comprises a single fragmented colony or several colonies); Nz = number of zooids. Values of zooid width in the holotype specimen of *C. voigtiana* (see Taylor 1980) are excluded because diagenetic crystal overgrowth has increased the measured value of this dimension.

		$\bar{x}$	SD	CV	r	Nc	Nz
C. thomasi	length	0·44	0·047	10·7	0·32–0·62	2–5*	102
	width	0·15	0·010	6·5	0·12–0·17	2–5*	97
C. voigtiana	length	0·50	0·071	14·3	0·39–0·78	8	82
	width	0·17	0·019	11·4	0·14–0·23	7	71

DIMENSIONS. See Table 1.

REMARKS. The holotype specimen (NGS256) consists of a shell encrusted by one large colony (Condra & Elias 1944: pl. 91, fig. 2) and several isolated, small groups of zooids, some preserving apparent colony origins (Fig. 1C). These small groups of zooids are interpreted as regenerated fragments of the larger colony (see below, p. 369). If this interpretation is correct, the large and small colonies together constitute a clone which might be regarded in its entirety as the holotype of the species.

Corynotrypa voigtiana (King 1850)

1848 *Stomatopora (Aulopora) dichotoma* Lamouroux; King: 6.
1850 *Aulopora Voigtiana* King: 31; pl. 3, fig. 13.
1857 *Hippothoa Voigtiana* (King) Kirkby: 217; pl. 7, figs 14–15.
1858 *Hippothoa Voigtiana* (King); Kirkby: 291; pl. 12, figs 14–15.
1861 *Hippothoa Voigtiana* (King); Geinitz: 120; pl. 20, figs 24–25.
1865 *Hippothoa Voigtiana* Kirkby [*sic*]; Schauroth: 29; pl. 1, fig. 3.
1977 *Hippothoa* ? *voigtiana* (King); Patttison: 36.
1980 *Stomatopora voigtiana* (King) Taylor: 621; fig. 1.

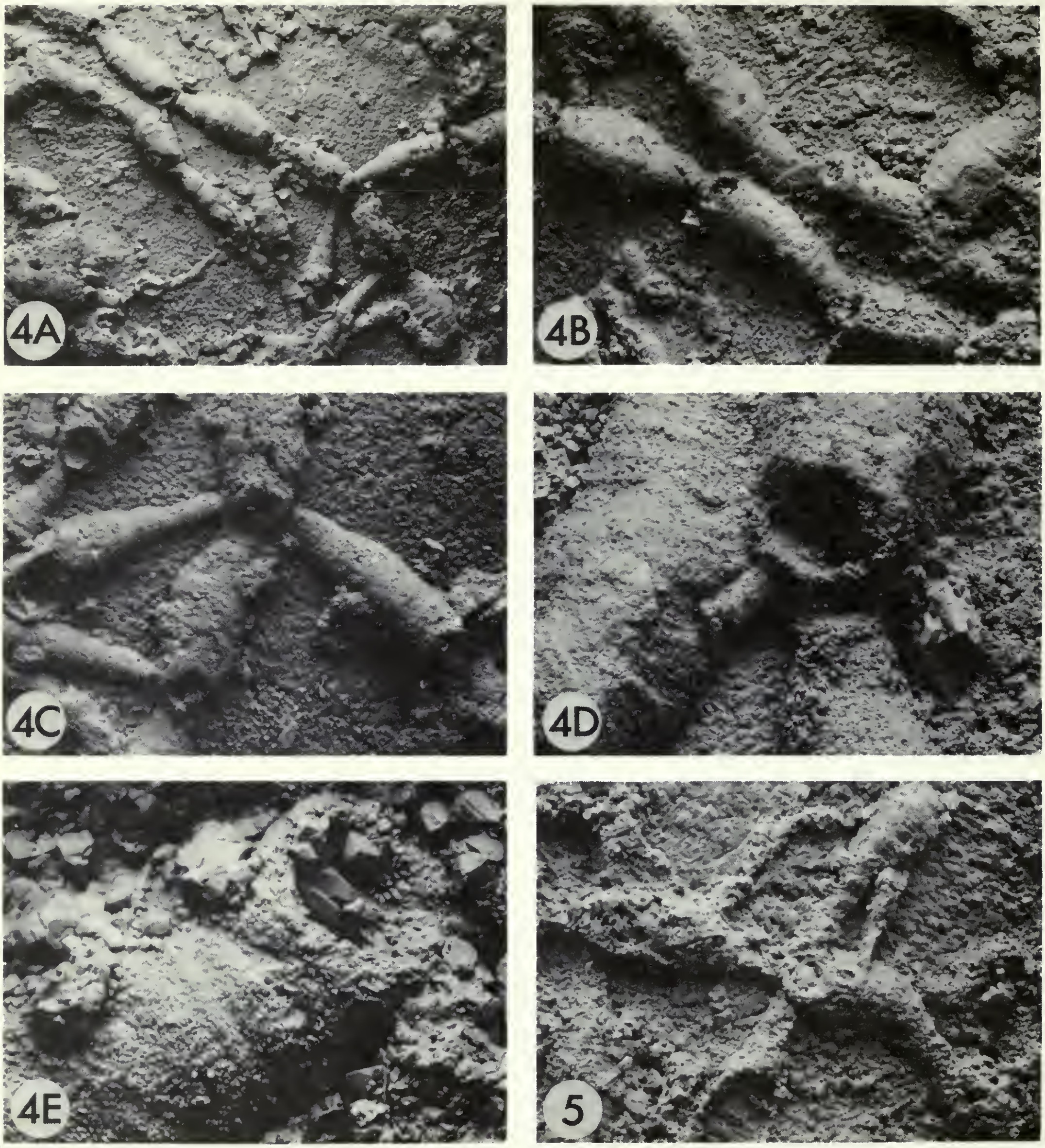
LECTOTYPE. UCG, King Collection B132. Middle Magnesian Limestone Reef, Upper Permian. Humbledon, Sunderland, Tyne and Wear. Colony of 16 zooids encrusting the exterior of a *Horridonia horrida*. Though King's description (1850) implies that more than one specimen of *C. voigtiana* was available to him, this is the only known syntype and was designated as the lectotype by Taylor (1980).

OTHER MATERIAL. BMNH PD6224–6. 'Middle Zechstein', Upper Permian. Pössneck, E. Germany. Presented by J. E. Lee 1885. Colonies encrusting crinoid columnals originally registered as part of BMNH E.1120.

NMC, Schauroth Collection 3541. Zechstein Dolomite, Upper Permian. Pössneck, E. Germany. Several bryozoan-encrusted crinoid columnals are registered under this number, including three better-preserved specimens here suffixed a, b and c (a and c are each fragmented into two pieces). It is not possible to match any of these specimens with Schauroth's (1865) sketchy illustration.

The specimen figured by Geinitz (1861) was amongst those from his collection in the Staatliches Museum für Mineralogie und Geologie zu Dresden destroyed during the Second World War (A. Prescher *in litt.*, March 1983).

Kirkby (1857, 1858) described several colonies from the Magnesian Limestone of Tunstall Hill in Sunderland. The whereabouts of these specimens is unknown; they could not be found among other Kirkby material in the collections of the Hancock Museum, Newcastle-upon-Tyne (A. M. Tynan *in litt.*, September 1983).



Figs 4–5 *Corynotrypa voigtiana* (King). 'Middle Zechstein', U. Permian; Pössneck, E. Germany. Fig. 4, BMNH PD6226. 4A, zooids encrusting a crinoid columnal, × 28; 4B, two subparallel branches, × 52; 4C, distolaterally-budded zooids initiating lateral branches with narrower proximal parts than distally-budded zooids, × 66; 4D, incompletely formed bud (kenozooid) terminating against the side of an existing zooid, × 160; 4E, zooidal aperture and non-pseudoporous frontal wall, × 260. Fig. 5, BMNH PD6225, typical poorly-preserved colony showing curved zooids and paired lateral branches, × 58.

Description. Colonies are encrusting and consist of branches of uniserially-arranged zooids (Fig. 4A, B). Branches may be gently curved. Daughter lateral branches arise as distolateral buds from zooids on a parent branch (Fig. 4C). These branches diverge from the parent branch at between 60° and 90° and may be paired, one either side of the parent branch. Branching frequency is variable; in some colonies (e.g. UCG B132) fewer than 15% of zooids give rise to a lateral branch, whereas in others (e.g. NMC3541a) about 40% of zooids give rise to a lateral branch. Crowding of branches may occur with numerous branch intersections, most resulting in the younger branch abutting against the side of the older branch without overgrowth (cf. Gardiner & Taylor 1982). Very short zooids without apertures are present at some branch intersections (Fig. 4D). These are presumed to be kenozooids resulting from restriction of growth. An apparent colony origin present in NMC3541c (Fig. 8) consists of two zooids joined at their narrow proximal ends and growing in opposite directions.

Zooids are small and elongate pyriform in shape, attaining their maximum width generally about two-thirds the distance along their lengths. Proximal parts of zooids are especially narrow in the distolaterally-budded zooids that form the first zooids in the lateral branches (Fig. 4C). Some zooids are curved and distinctly asymmetrical. A few straggly zooids are present in BMNH PD6226 and may be abortive. Well-preserved frontal walls lack pseudopores and are marked by transverse wrinkles (Fig. 4D). Frontal walls are commonly poorly preserved and crystalline (Fig. 5). Zooidal apertures are terminal, circular or elliptical and transversely elongate, and small (*c.* 0·06–0·08 mm in diameter). Peristomes have not been observed. Regular astogenetic variation in zooid size has not been detected.

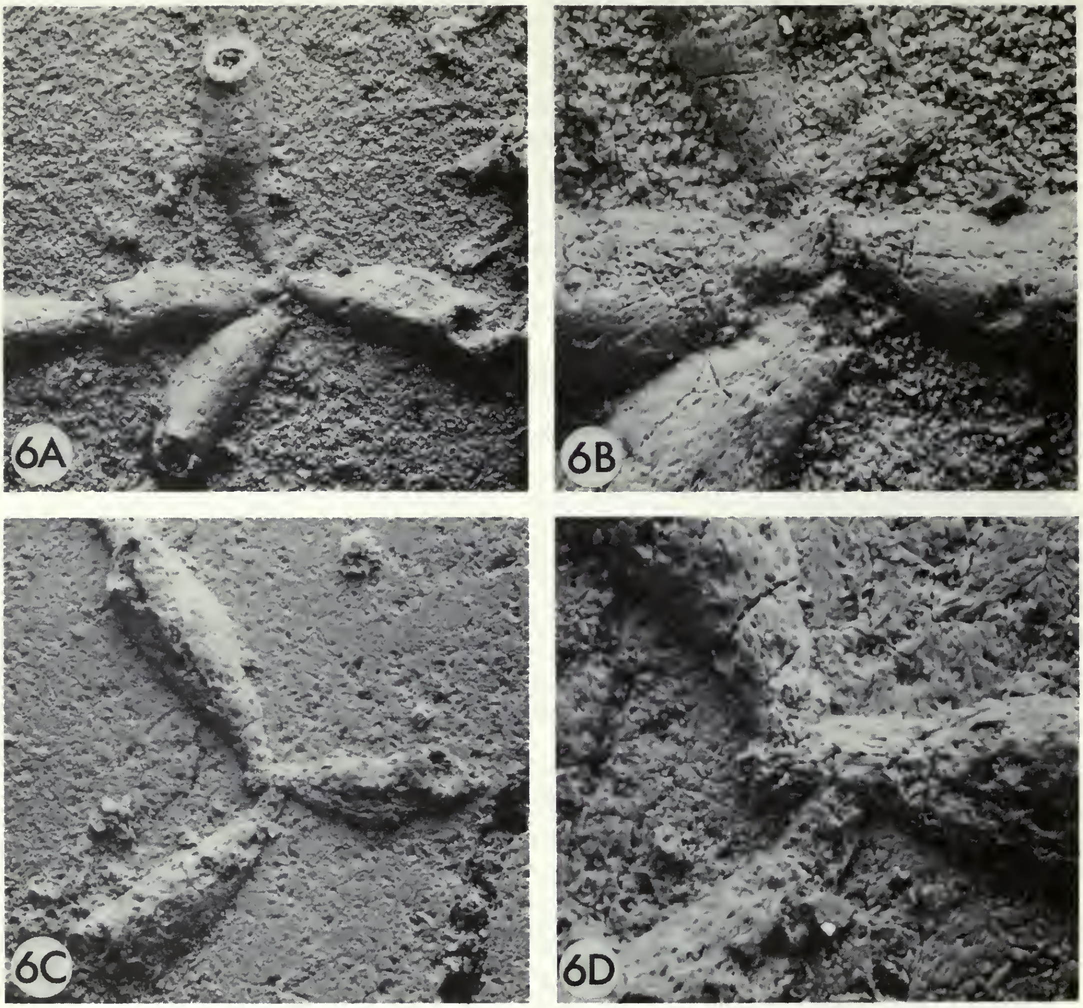
DIMENSIONS. See Table 1.

REMARKS. An earlier revision (Taylor 1980) of this species was based on a restudy of the lectotype, the only specimen known to be in existence at that time. In this specimen coarse preservation obscures details of wall structure and the presence or absence of pseudopores could not be established. The comparatively broad proximal ends of the zooids (probably due to diagenetic crystal overgrowth) led to the species being incorrectly assigned to *Stomatopora* Bronn. Newly available material shows very clearly the absence of pseudopores in well-preserved frontal walls and the narrow proximal ends of the zooids; these features allow reassignment to *Corynotrypa* Bassler. This new material first came to light among specimens borrowed from the Schauroth Collection in the NMC; they were found encrusting columnals of *Cyathocrinus* from the Zechstein of Pössneck. Examination of crinoid columnals from the same locality in the Echinoderm Collection of the BMNH led to the discovery of three further colonies (BMNH PD6224–6) of *C. voigtiana*, including an especially well-preserved colony (PD6226).

C. voigtiana is very similar to *C. thomasi* but can be distinguished by the slightly longer and wider zooids (Table 1), which may be transversely wrinkled. Lateral branches are more frequent in most *C. voigtiana* colonies.

Propagation in *Corynotrypa*

Sexual reproduction in bryozoans results in free-swimming larvae whose settlement on a firm substrate is the first stage in the formation of the majority of colonies. The founder zooid of these sexually-produced colonies, the ancestrula, is usually smaller than later zooids and may be morphologically distinctive. The ancestrula in *Corynotrypa* has not been illustrated previously, though Dzik (1981: text-fig. 7a) gives an outline diagram of a partly-preserved ancestrula in *C.* cf. *schucherti* Bassler. Dzik (1981: text-fig. 4b) also figures the ancestrula of the related genus *Wolinella* Dzik which has a bulb-like proximal end, the protoecium (= proancestrula, primary disc or basal disc). Protoecia are a feature of the ancestrula in most or all stenolaemate bryozoans and may be a useful skeletal synapomorphy for the Class Stenolaemata. Examination of numerous Ordovician to Permian species of *Corynotrypa* in the BMNH collections has revealed only two examples of zooids that could be positively identified as ancestrulae by the presence of a protoecium. Both are in colonies of *C. dissimilis* (Vine) from the Silurian (BMNH R1900a, D36468). The protoecium in *C. dissimilis* (Figs 10, 11) is somewhat wider than the remainder of the ancestrula and resembles protoecia in post-Palaeozoic cyclostomes (e.g. Gardiner & Taylor 1982: fig. 1A).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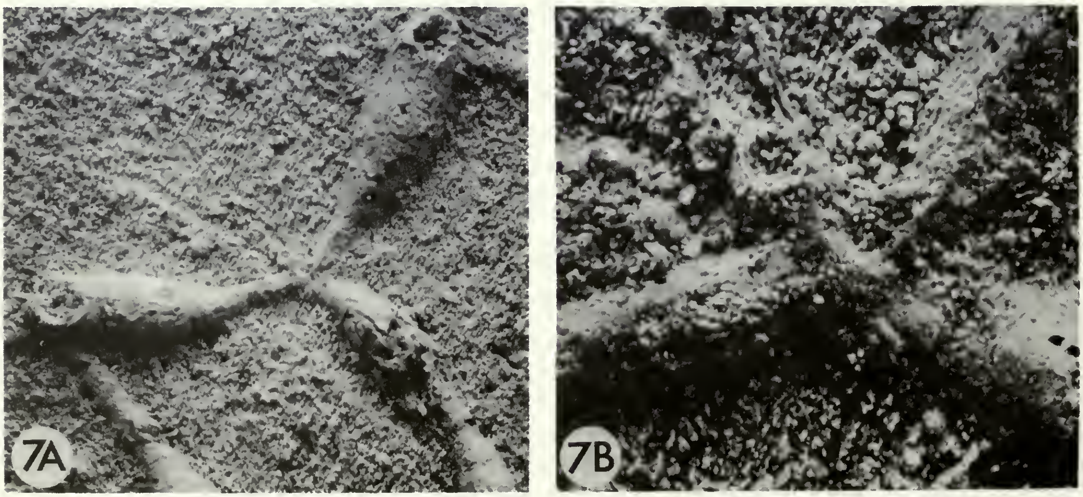
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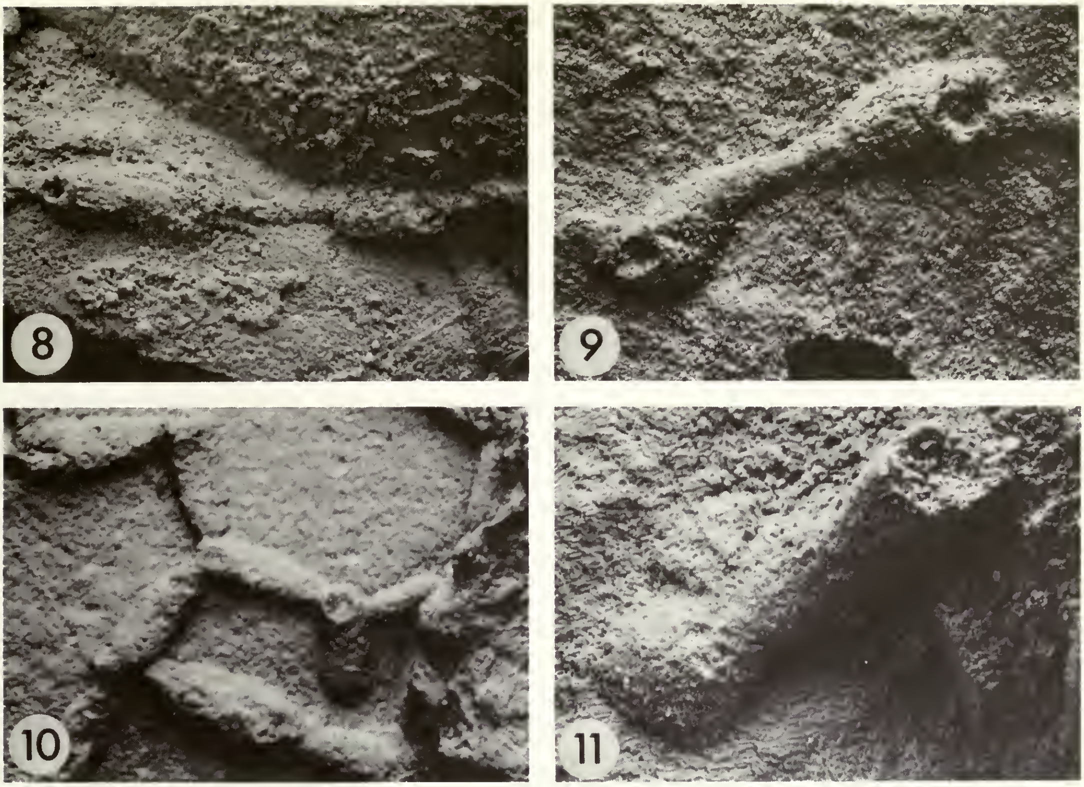

Figs 8–11 Origins of colony growth and ancestrulae in *Corynotrypa*. Fig. 8, *C. voigtiana* (King), NMC Schauroth Collection 3541c; Zechstein Dolomite, Upper Permian; Pössneck, E. Germany. Two zooids growing in opposite directions, × 52. Fig. 9, *C. inflata* (Hall), BMNH D5851a; Lorraine Group, U. Ordovician; Cincinnati, Ohio, U.S.A. Two zooids growing in opposite directions, × 54. Fig. 10, *C. dissimilis* (Vine), BMNH D36468; U. Silurian; Gotland. Ancestrula with protoecium just right of centre, × 20. Fig. 11, *C. dissimilis* (Vine), BMNH R1900a; Wenlock Limestone, Silurian; Dudley, England. Ancestrula with long peristome and bulbous protoecium (lower left), × 67.

Ancestrulae with protoecia could not be located in most species of *Corynotrypa*, despite the fact that encrusting colonies of *Corynotrypa* are unlike many erect bryozoans in which proximal parts are overgrown by later zooids or can be dissociated from the bulk of the colony prior to burial. When identifiable, apparent colony origins were instead represented by a group of 2–4 diverging or radiating zooids joined at their narrow proximal ends (Figs 6–9). Structures of this type were found in *Corynotrypa* sp. from the M. Ordovician of

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Figs 6–7 Origins of colony growth in *Corynotrypa thomasi* Condra & Elias. Fig. 6, NGS 256; Spring Branch Limestone Member, Lecompton Formation, Shawnee Group, Pennsylvanian (U. Carboniferous); Snyderville Quarry, Nehawka, Nebraska, U.S.A. 6A, group of four radiating zooids at the origin of the large colony shown in Fig. 1A, × 60; 6B, detail of central area showing irregularities, fracturing, and the presence of an additional partial zooid (upper right), × 150; 6C, group of three zooids at the origin of the small colony shown in Fig. 1C; × 72; 6D, detail of central area showing broken proximal end of zooid on the right which has apparently formed two proximolateral buds, × 210. Fig. 7, BMNH PD6023; Bangor Limestone (lower), Chesterian, Mississippian (L. Carboniferous); Fox Trap, Colbert County, Alabama, U.S.A. 7A, group of three radiating zooids at the origin of colony growth, × 67; 7B, detail of central area showing open proximal end of the smallest of these three zooids, × 330.

Virginia (BMNH PD5776), *C. inflata* (Hall) from the U. Ordovician of Cincinnati (BMNH D5851a, Fig. 9), *C. dissimilis* from the Silurian of England (BMNH 60521), *C. thomasi* (Figs 6, 7) and *C. voigtiana* (Fig. 8). Initially it was thought that one zooid within each group was the ancestrula or, alternatively, that the group as a whole constituted an ancestrular complex. However, the lack of a protoecium is evidence against both of these interpretations. Ancestrular complexes, known in several cheilostomes (Cook 1973), are as yet undescribed from stenolaemates (though more than one zooid may bud from the protoecium in some cyclostomes, Illies 1974), and the variability in the number of zooids (2–4) comprising the group in *C. thomasi* does not match with expectations for an ancestrular complex. Finally, the occurrence of these apparent colony origins in a species (*C. dissimilis*) known to have an ancestrula with a protoecium demonstrates that, in this species at least, none of the radiating zooids is the ancestrula. Detailed scanning electron microscope (SEM) studies revealed growth irregularities at the loci of the groups of radiating zooids. There are indications of fracturing at the proximal ends of the zooids, and short, broken segments of additional zooids may be present (Fig. 6B). This suggests that these colony origins represent damaged parts of colonies repaired by regenerative budding of zooids in proximal and other directions. Similar structures have been described in the uniserial cheilostome *Pyriporopsis*? *catenularia* (see Cheetham & Cook *in* Boardman *et al.* 1983: figs 76, 1a). The growth pattern

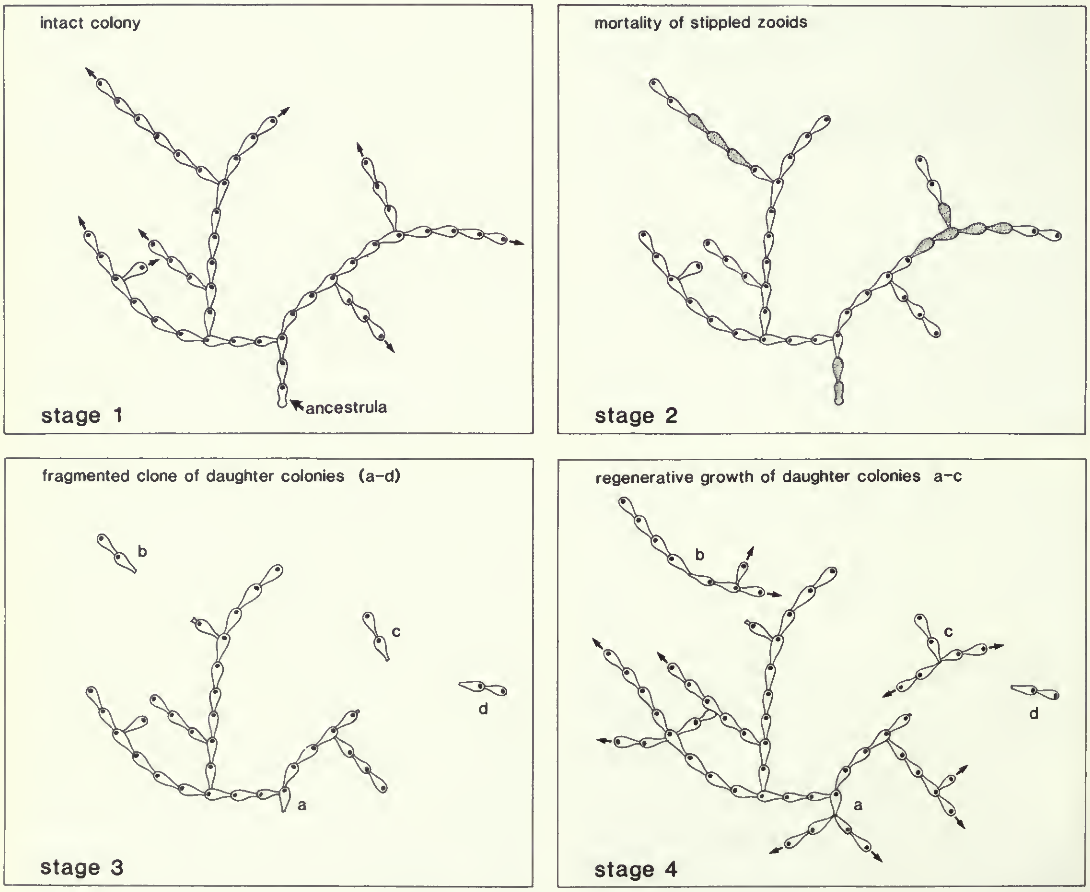
intact colony
ancestrula
stage 1
mortality of stippled zooids
stage 2
fragmented clone of daughter colonies (a–d)
b
c
d
a
stage 3
regenerative growth of daughter colonies a–c
b
c
d
a
stage 4

Fig. 12 Model of clonal propagation by colony fragmentation in *Corynotrypa*. Arrows indicate active growing tips.

of *P.? catenularia* colonies closely resembles that of *Corynotrypa* and, as in *Corynotrypa*, the ancestrula is unknown; a possible ancestrula in *P.? catenularia* figured by Cheetham & Cook (*in* Boardman *et al.* 1983: fig. 76, 5) proved, when examined using SEM, to have irregularities suggestive of fracturing and repair.

Encrusting colonies of *Pyriporopsis*? and *Corynotrypa* have runner-like growth forms well suited to the location of spatial refuges on the substrate (Buss 1979, Jackson 1979). However, such fugitive colonies are likely to be poorly committed to the defence of individual zooids within the colony. Therefore, zooids may be highly ephemeral. This would have two consequences: firstly, there would be a low probability of the earliest zooids (including the ancestrula) remaining intact in old, large colonies; and secondly, fractured branches, at least some of which might be repaired, would be of frequent occurrence.

The holotype specimen of *Corynotrypa thomasi* consists of a shell encrusted by a large colony (Fig. 1A), and several isolated small colonies each comprising only a few zooids (Fig. 1C). Some of these small colonies originate from groups of radiating zooids of the kind interpreted as products of regeneration following damage. It seems probable that these small colonies are ramets (*sensu* Harper 1977) formed by fragmentation of the larger colony. Fig. 12 depicts diagrammatically the fragmentation process envisaged. While some of the fragments may have ceased growth, others evidently retained viability and, in addition to resuming normal distal budding, were able to produce proximally growing buds to repair their fractured proximal parts. Fragmentation is presumed to have been caused by external agencies among which grazing of the substratum surface could have been important (cf. Jackson & Winston 1981).

Recent interest has been shown in fragmentation as a means of asexual or clonal propagation in colonial animals (e.g. Highsmith 1982, Hughes 1983). Clonal propagation in bryozoans seems to be associated mainly with erect and free-living colonies (e.g. Marcus & Marcus 1962, McKinney 1983, Winston 1983 and Hakannson & Thomsen in press – paper presented at the 6th Conference of the International Bryozoology Association, Vienna, July 1983). Jackson & Winston (1981), however, describe examples of colony fission in encrusting cheilostomes on fouling panels placed on Caribbean reefs. In erect and free-living bryozoans

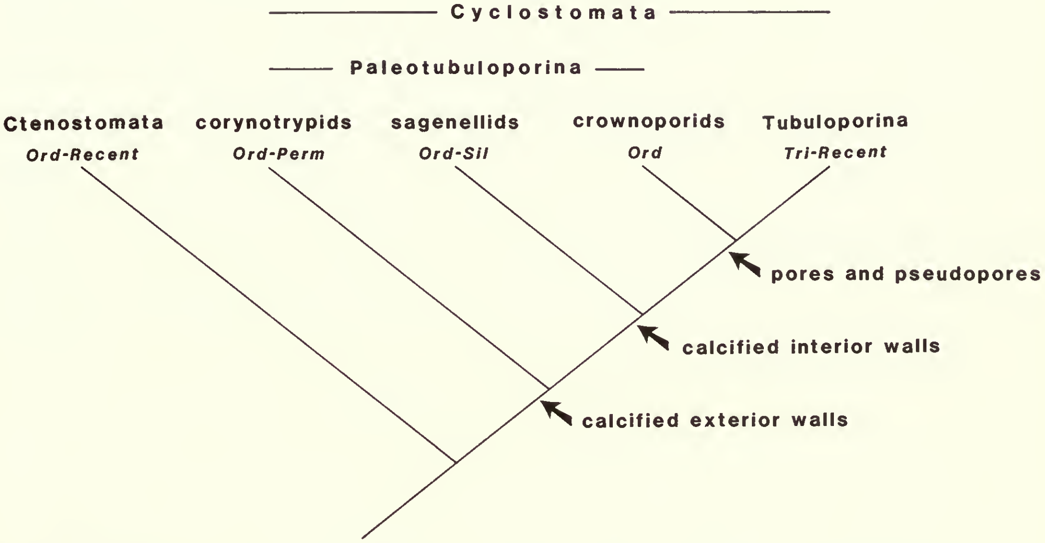

Fig. 13 Tentative, simplified cladogram showing inferred relationships between Palaeozoic cyclostomes and primitive post-Palaeozoic cyclostomes (Tubuloporina). The Ctenostomata are regarded as the primitive sister group of the Cyclostomata (see Larwood & Taylor 1979).

the individual fragments (daughter colonies) of the clone commonly become spatially separated after breakage. Here clonal propagation can have a role in dispersal, colonization of virgin environments, and increasing genotype longevity. Except in cases where the substratum itself is broken and the fragments separated, clonal propagation in encrusting bryozoans would appear to have no significance in these roles. Instead it seems merely to be a consequence of the ability of colonies to survive fission. Nevertheless, recognizing the possibility of clonal propagation in encrusters such as *Corynotrypa* is of importance during studies of population abundance, overgrowth relationships, between colony morphological variation, etc.

Remarks on phylogeny

In the only major studies, Palaeozoic cyclostomes have been classified within the Suborder Paleotubuloporina Brood, 1973 (Brood 1973, 1975; Dzik 1981). However, the morphological basis of this suborder is unclear. Brood's original diagnosis (Brood 1973) emphasizes the absence of interzooidal pores and pseudopores (though pseudopore-like structures were described in one genus), whereas Dzik's amended diagnosis (Dzik 1981) stresses the presence of interzooidal pores ('communication canals').

A review of existing morphological descriptions suggests that Palaeozoic cyclostomes divide into three informal groups: corynotrypids, sagenellids and crownoporids. These correspond approximately to the families Corynotrypidae Dzik, 1981, Sagenellidae Brood, 1975 (excluding *Corynotrypa*) and Crownoporidae Ross, 1967 (= Kukersellidae Brood, 1975 which was incorrectly proposed to replace Crownoporidae following the recognition of *Crownopora* Ross, 1967 as a subjective junior synonym of *Kukersella* Toots, 1952). Corynotrypids lack calcified interior walls and consequently have complete continuity between the zooecial chambers of contiguous zooids; sagenellids have calcified interior walls separating contiguous zooids but these walls are non-porous and the exterior walls lack pseudopores (the paired frontal pores of *Sagenella consimilis* (Lonsdale) are probably not pseudopores); crownoporids have calcified interior walls with pores and/or exterior walls with pseudopores.

Of the three groups of Palaeozoic cyclostomes, crownoporids most closely and corynotrypids least closely resemble post-Palaeozoic cyclostomes. Although there are broad similarities in colony-form and zooid shape between many corynotrypids and primitive Mesozoic stomatoporids, these similarities may be poor indicators of phylogenetic affinity. Stomatoporids differ from corynotrypids in having well-developed calcified interior walls with pores, and exterior walls with pseudopores. In all Jurassic stomatoporids branch multiplication occurs by bifurcation and not lateral branching as in corynotrypids. Regenerative proximal budding of zooids has not been observed in Jurassic stomatoporids. Therefore, evolution of primitive post-Palaeozoic cyclostomes from a late Palaeozoic corynotrypid like *Corynotrypa voigtiana* seems unlikely. Primitive post-Palaeozoic cyclostomes may have closer affinities with crownoporids with which they share porous interior walls and pseudoporous exterior walls (Dzik 1981). These similarities are assumed to be homologous (synapomorphies) rather than convergent, though knowledge of crownoporid morphology is deficient and the group may encompass a wide variety of morphologies. Favoured relationships are expressed in a tentative cladogram (Fig. 13). A problem of this hypothesis of relationships is the large hiatus in the fossil record between crownoporids, which are possibly restricted to the Ordovician, and the first post-Palaeozoic cyclostomes which appear in the late Triassic (Prantl 1938, Bizzarini & Braga 1981). Poor preservation potential may partly explain this gap. Palaeozoic cyclostomes have thin colonies that contrast with those of the other Palaeozoic stenolaemate orders. These thin colonies are both delicate and easily overlooked. Therefore resolution of phylogenetic relationships should be clarified not only by more complete morphological study of known species, but also by the search for further encrusting cyclostomes attached to shell substrates and erect cyclostomes within fine-grained sediments.

Acknowledgements

I am grateful to Mrs A. J. Burgess-Faulkner for first noticing the colony of *Corynotrypa thomasi* among material collected from Fox Trap, Alabama under the expert field guidance of Dr F. K. McKinney (Appalachian State University). Dr G. Aumann (NMC) and Dr R. K. Pabian (NGS) generously arranged loans of specimens in their care, and Dr A. Prescher (Dresden) and Mr A. M. Tynan (Newcastle-upon-Tyne) kindly conducted searches for additional specimens. Dr F. K. McKinney and other bryozoologists provided helpful discussion, and Miss P. L. Cook criticized the manuscript.

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Redescription of *Eurycephalochelys*, a trionychid turtle from the Lower Eocene of England

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Synopsis

Since Moody & Walker first described *Eurycephalochelys fowleri* in 1970, two more skulls have been discovered in the Bracklesham Series (Lower Eocene) of Sussex. These specimens, while supporting the original description of the species and validating the restoration attempted in the earlier publication, also provide further data on its morphology, size and stratigraphical range. A re-diagnosis is given.

Introduction

Continued collecting from the shoreline deposits of Bracklesham Bay at East Wittering by Mr R. Fowler has yielded several testudinate specimens. Amongst these are limbs and shells of both podocnemid and trionychid turtles and two skulls referable to *Eurycephalochelys fowleri*; Mr Fowler, who also discovered the holotype, has presented these skulls to the Department of Palaeontology, British Museum (Natural History). The first (R8694), virtually complete, was found in an oyster bed within the Cakeham Beds (Curry *et al.* 1977), whilst the second (R8695), represented only by the bones of the ventral or palatal surface, was found in the Nipa Bed at the base of the Cakeham Beds (Figs 1, 2).

The discovery of the two specimens, particularly R8695, confirms the existence in Cuisian times of a trionychid far larger than any other described species, fossil or extant. The two skulls show most of the characters described in 1970 by Moody & Walker.

Description

Order **TESTUDINES**

Suborder **CRYPTODIRA**

Superfamily **TRIONYCHOIDEA** Fitzinger 1826

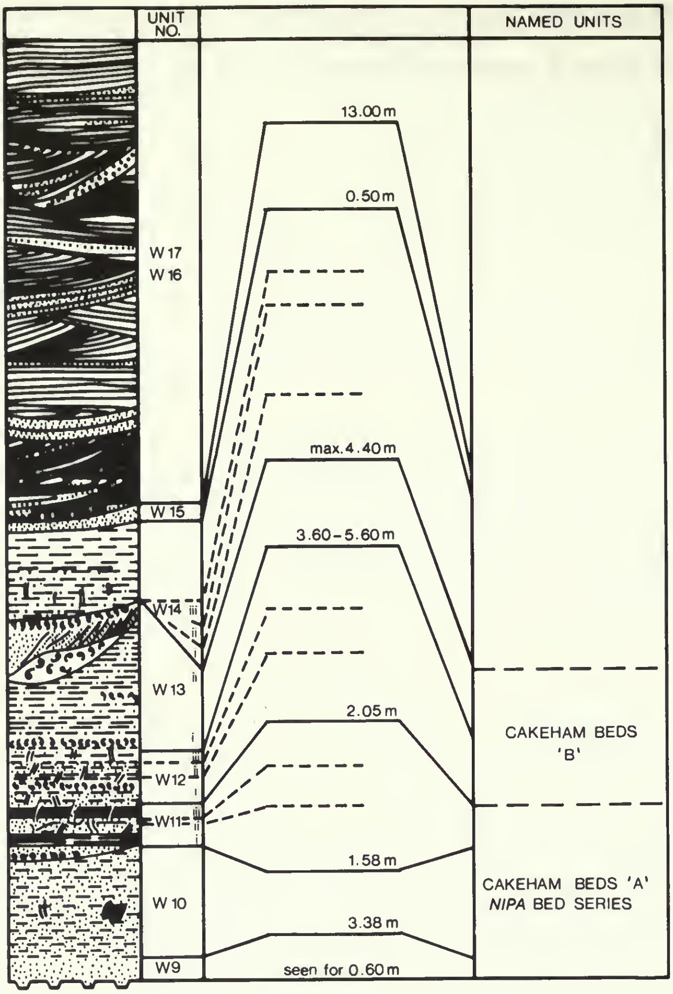
Family **TRIONYCHIDAE** Fitzinger 1826

Genus ***EURYCEPHALOCHELYS*** Moody & Walker 1970

TYPE SPECIES. *Eurycephalochelys fowleri* Moody & Walker 1970.

EMENDED DIAGNOSIS. Quadrate condyle situated relatively far back, so that it lies behind stapedial foramen, in line with opening of foramen magnum, with posterior edge in line with maximum width of basioccipital; occipital condyle projecting some distance behind it; inclination of forwardly-directed flange of quadrate more horizontal than in other trionychids. Canalis alveolaris superior (internal maxillary foramen) situated at base of

Bull. Br. Mus. nat. Hist. (Geol.) **38** (5): 373–380 Issued 31 January 1985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NAMED UNITS
13.00 m
0.50 m
max. 4.40 m
3.60-5.60 m
2.05 m
1.58 m
3.38 m
seen for 0.60 m
W 17
W 16
W 15
W 14
W 13
W 12
W 11
W 10
W 9
CAKEHAM BEDS 'B'
CAKEHAM BEDS 'A'
NIPA BED SERIES

Fig. 1 Upper part of the Wittering Division stratigraphy (after Curry *et al.*, 1977).

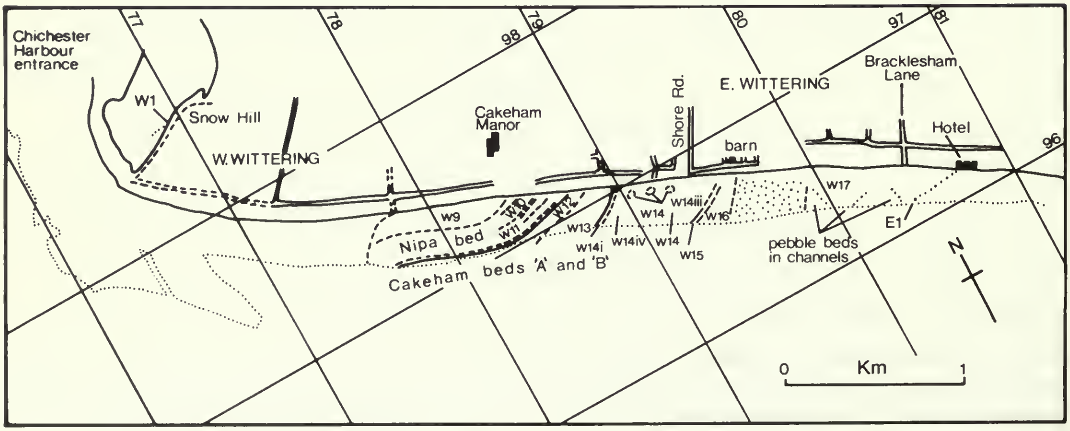
Chichester Harbour entrance
W1
Snow Hill
W. WITTERING
Cakeham Manor
Shore Rd.
E. WITTERING
Bracklesham Lane
barn
Hotel
Nipa bed
Cakeham beds 'A' and 'B'
W9
W10
W11
W12
W13
W14i
W14iv
W14
W14iii
W15
W16
W17
E1
pebble beds in channels
N
0 Km 1
77
78
79
80
81
98
97
96

Fig. 2 Map of Wittering foreshore exposures, to show the site of the Cakeham Beds (after Curry *et al.*, 1977).

vertically rising wall of maxilla. Anterior opening of foramen palatinum posterius situated to side of ascending process of palatine and not enclosed in base of that bone as in *Cyclanorbis*. Jugal bar originates well below lowest point of orbital margin. Foramen magnum, and brain cavity immediately anterior to it, rounded. Snout region short and broad, with distance from tip of premaxilla to front of orbit much greater than anteroposterior diameter of orbit. Maximum width of skull across jugal bars equal to width across articular region of quadrates. Maxilla very deep, being two-thirds as deep as vertical diameter of orbit. Orbits small, somewhat longer than high and directed upwards and slightly forwards. Area of quadrate exposed on dorsal surface not larger than area of prootic but of approximately equal size. Tympanic cavity shallow and triangular in outline. Walls of choanal vault very steep and well-rounded.

Eurycephalochelys fowleri Moody & Walker 1970

HOLOTYPE. Incomplete skull without lower jaw (R8445).

REFERRED SPECIMENS. An almost complete skull without lower jaw (R8694; Figs 3–5), and the palatal region of a very large skull (R8695). Casts of these specimens are in the collection of Mr R. Fowler, Moschatel, Church Road, East Wittering, Sussex.

OCCURRENCE. The Wittering Formation, Bracklesham Series, Cuisian (Lower Eocene); foreshore, East Wittering, Sussex, England.

DESCRIPTION of new material. Of the two new specimens R8694 is exceedingly well preserved and, apart from some dorsoventral crushing of the prefrontal region, is almost perfect. It exhibits a profile closely resembling that of the original reconstruction (Moody & Walker 1970: 508) although some detailed differences can be observed. In dorsal view (Fig. 3) it can be seen that the width of the interorbital bar, at its narrowest point, is greater than the maximum dorsoventral measurement of the orbit. Further, the jugal bar is more curved than that depicted in the original reconstruction, and therefore enhances the overall broad appearance of the skull. Within the orbits the canalis alveolaris superior (internal maxillary foramen) is unquestionably situated in the floor of the orbit whereas that of the holotype is positioned in the medial wall of the maxilla. However, the foramen is still sited in a more lateral position than any known trionychid. The difference could be explained by either erosion of the holotype or by individual variation. The lateral surface of the parietal is more steeply inclined in R8694, and the parietal/supraoccipital spine, absent in the holotype, is more massive than that of most recent forms and lacks the sharp undercut edge they possess. It is unfortunate that the sutures in this skull are almost completely closed, for it makes it impossible to confirm that there is no sutural contact between the prootic and the opisthotic on the dorsal surface, nor is it possible to make any further comments on the relative size of the prootic and quadrate in that view.

In lateral view (Fig. 4) the skull shows the same steep facial angle, and with a complete interorbital bar it can now be said that the depth of the maxilla is much greater than the vertical diameter of the orbit. As the jugal bar is present it is seen to be very narrow dorsoventrally, being approximately one-third of the depth of the maxilla below the orbit. The stapedial foramen of R8694 does not form such an obtuse angle with the condyle of the quadrate as in the type specimen, nor does the forwardly-directed flange of the quadrate lie so close to the horizontal.

The palatal surface of R8694 (Fig. 5) is by far the most complete known and shows that the intermaxillary foramen was of moderate size and approximately the same length as the intermaxillary suture. The morphology of the choanal vault area appears to indicate a condition similar to that found in *Cyclanorbis*, in that the vomer would not have overlain the palatines to any degree and in consequence did not produce the strong central vomerial ridge characteristic of *Trionyx*. The region differs from that of the reconstruction in that the anterior margins of the choanae are placed more posteriorly than in most trionychid genera

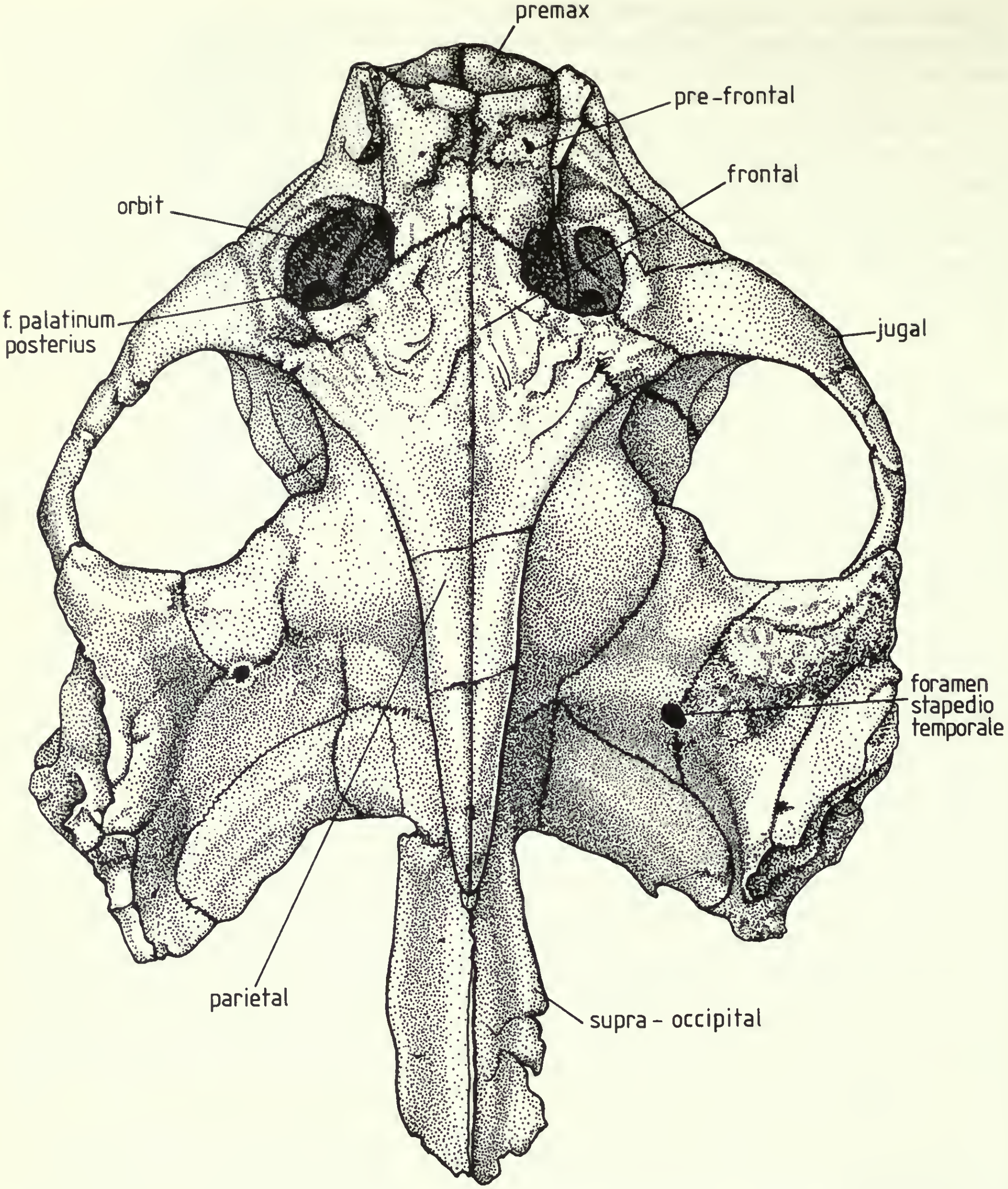
premax
pre-frontal
frontal
orbit
f. palatinum posterius
jugal
foramen stapedio temporale
parietal
supra - occipital

Fig. 3 *Eurycephalochelys fowleri* Moody & Walker, R8694. Dorsal view of skull, × 0·75.

and probably represent the primitive condition. In contrast the foramen palatinum posterius is in the normal position connecting internally, via a short canal, with an anterior foramen sited to the side of the ascending process of the palatine. This condition is more typical of *Trionyx* and *Cycloderma* than of *Cyclanorbis*, in which the internal formen occurs at the base of the process. The posterior openings of the foramen posterior canalis carotici interni are not visible in this view. The foramen is covered by the pterygoid and in this respect is similar to *Chitra*. In the original restoration, it was shown in the normal position and was therefore incorrectly placed.

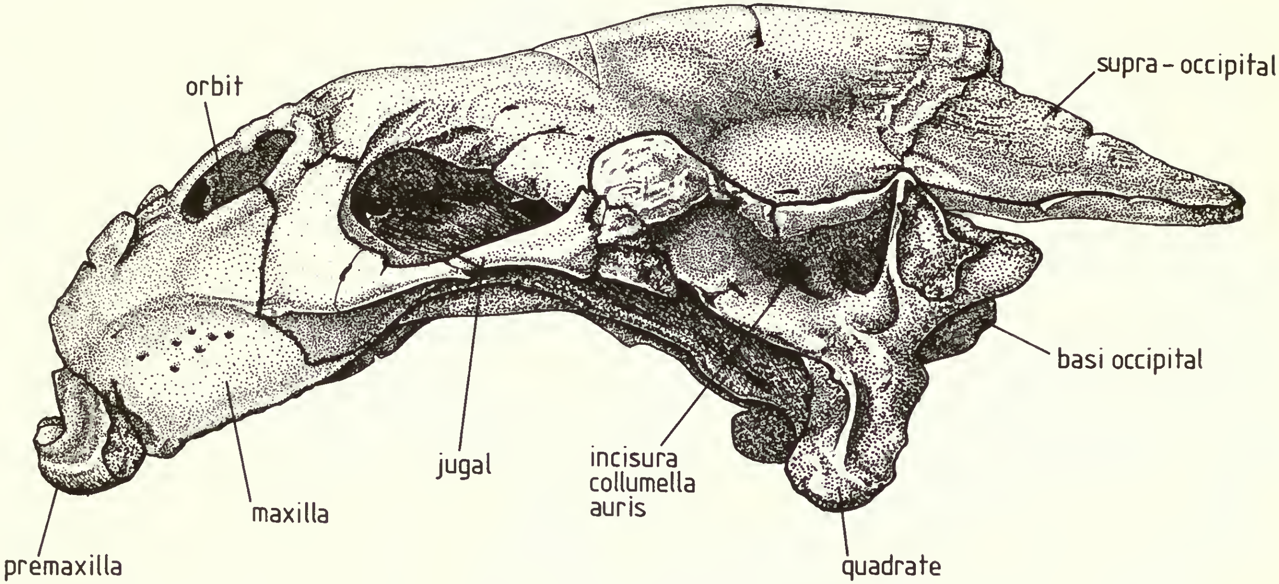
orbit
supra - occipital
basi occipital
jugal
incisura collumella auris
maxilla
premaxilla
quadrate

Fig. 4 *Eurycephalochelys fowleri* Moody & Walker, R8694. Left lateral view of skull, × 0·75.

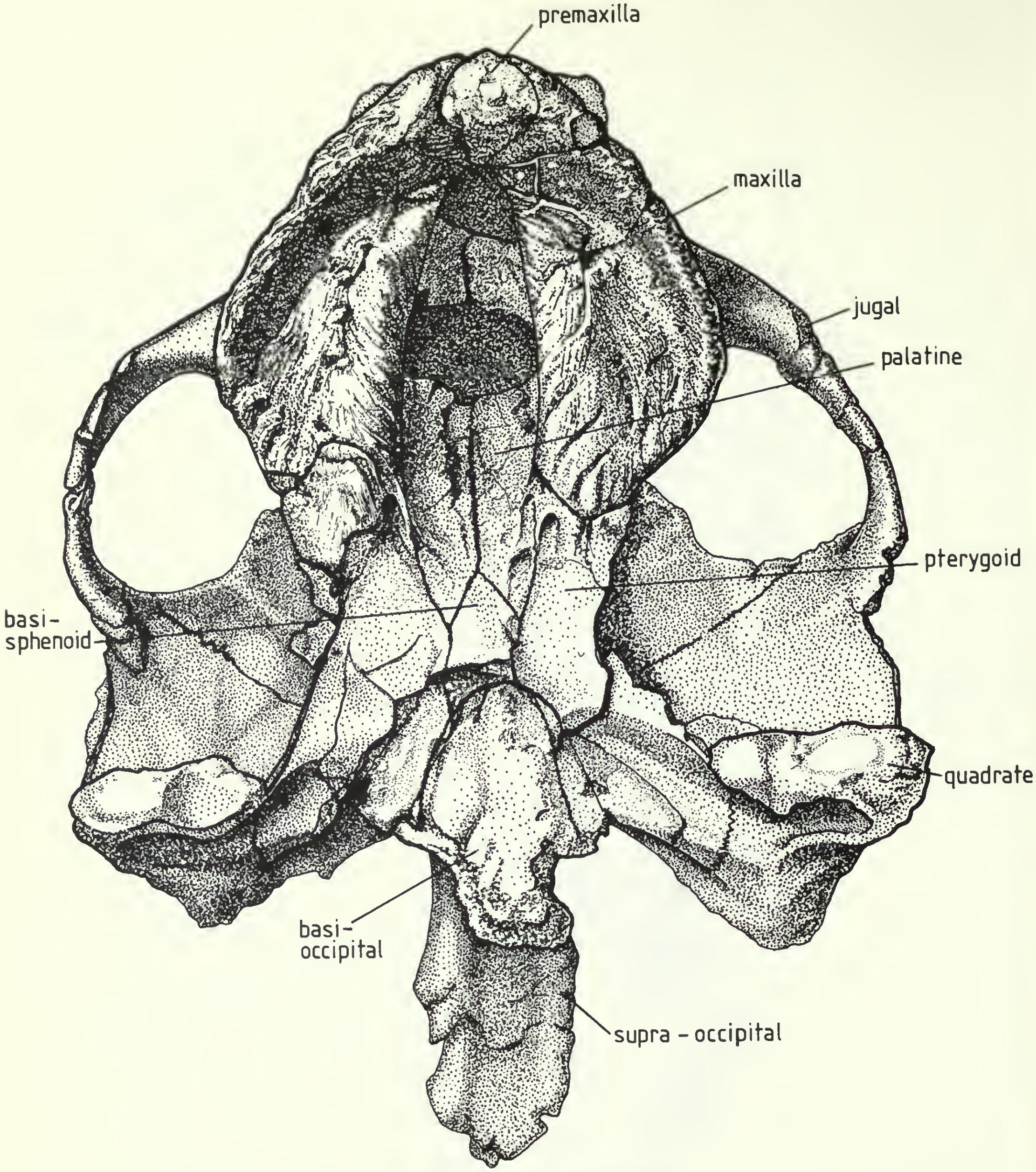
premaxilla
maxilla
jugal
palatine
pterygoid
basi-
sphenoid
quadrate
basi-
occipital
supra - occipital

Fig. 5 *Eurycephalochelys fowleri* Moody & Walker, R8694. Palatal view of skull, × 0·75.

In occipital view there is a well-developed depression on either side of the foramen magnum. Each is centred on the posterior edge of the exoccipital and to a lesser extent the opisthotic. This region is rather variable in trionychids, but no modern form appears to have developed such a depression in which the opisthotic overhangs the dorsal surface. In fact in *Cycloderma* and *Chitra* there is no comparable feature and in the other trionychids it is represented by a shelf which can be clearly seen in dorsal view. The fenestra postotica is unrestricted, with no indication of an ascending process on the pterygoid. This is at variance with the holotype, but Loveridge & Williams (1954) show that this could be a variable character, at least within *Trionyx*.

MEASUREMENTS (in millimetres)

(E = estimated)	R8694	R8695	R8445 (Holotype)
Actual length premaxilla – occipital condyle	167	234 (E)	157
Maximum length premaxilla – supra-occipital spine	212	–	215 (E)
Width across quadrates	147	207	132
Width across external nares	34	42	23
Anterior margin of orbit to premaxilla	50	–	42
Minimum depth of maxilla below orbit	31·5	42 (E)	30
Maximum length of orbit	24	–	26
Maximum depth of orbit	22	–	22
Estimated length of anterior palatine foramen	16	–	8
Estimated length of intermaxillary suture	19	–	13
Estimated length of choanae	20	–	17
Maximum width across maxilla in palatal view	89	116 (E)	87
Maximum width of articular surface of quadrate	34·5	52	29
Maximum width across jugals	144	–	–
Minimum width of interobital bar	22	–	–
Tip of premaxilla to maximum width of maxilla	47	55	43
Maximum width across orbits	59	70 (E)	54
Minimum width across pterygoids	58 (E)	78	54 (E)

COMPARISONS. There can be little doubt that *Eurycephalochelys* more closely resembles *Trionyx* than any other fossil or Recent trionychid. It does, however, bear comparison with both *Cyclanorbis* and *Cycloderma*. For whereas the shape of the external nares is broader than high the reverse condition is accepted as normal for *Trionyx*. In palatal view the intermaxillary foramen is of moderate size, approximating to the length of the intermaxillary suture. This condition is similar to that of *Trionyx, Cycloderma* and *Lissemys*, but differs from that in *Cyclanorbis* and *Chitra* where the foramen is either highly reduced or even absent. The vomer, although missing, was probably not as well developed as that of *Trionyx* or *Chitra*, and there is no indication of any marked vomerial ridge on the roof of the choanal vault region. *Cyclanorbis, Lissemys* and to a lesser extent *Cycloderma* exhibit a weak vomerial ridge. The posterior openings of the foramen posterior canalis carotici interni cannot be seen in palatal view, and in this respect *Eurycephalochelys* resembles *Chitra* and no other trionychid. In occipital view it bears a distinct resemblance to *Trionyx*, but the depressions for the attachment of the cervical musculature on either side of the foramen magnum are rather better developed than in other trionychids. The closest comparison to this condition has been observed in certain specimens of *T. cartilagineus* (Boddaert) but even in this species it is not so pronounced as in *Eurycephalochelys*. The fenestra postotica is not restricted in R8694, and although this contrasts with the limited development of the ascending process of the pterygoid in the holotype, Loveridge & Williams (1957) have noted that specimens referred to *T. triunguis* (Forskål) exhibit similar intraspecific variation. Within the orbit, the position of the canalis alveolaris superior (internal maxillary foramen) is more laterally placed than in other trionychids. This feature appears to be somewhat variable, however, for in the holotype this foramen is situated in the medial wall of the maxilla. Further, the anterior opening of the foramen palatinum runs to the external side of the ascending process of the palatine, as in *Trionyx* and *Cycloderma*, whereas in *Cyclanorbis* and *Lissemys* it exits through the centre of that bone. The structure of the quadrate remains enigmatic, for the stapedial foramen lies behind that of the holotype; in fact it is only slightly more forward than in any trionychid other than *Chitra*. Although some crushing has affected both the holotype and R8694 it is thought that the variation in this character is intraspecific rather than preservational.

Conclusions

Since the original description of *Eurycephalochelys fowleri*, a major work on the testudinates of the Cretaceous and Tertiary deposits of France has been presented by de Broin (1977). In this paper the author makes comparisons between the various fossil trionychids of Belgium, France and England, and attempts in several places to link the European genera and species with those of the rest of the world. In dealing with fragmentary material from the Palaeocene and Lower Eocene deposits of the Paris Basin, she associates the European species *Trionyx vittatus* Pomel (1847) with the North American genus *Palaeotrionyx* Schmidt (1945). Her arguments for this association are based essentially upon shell ornament, the same reasoning leading her to refer *T. levalensis* Dollo to the same genus.

De Broin (1977) has followed us (Moody & Walker 1970) in regarding *T. levalensis* as a nomen nudum, but disagrees with us in inferring that *T. levalensis* and *E. fowleri* are conspecific. We believe this is incorrect, for whilst we appreciate that a case may exist for the association of fragmentary postcranial material on shell ornament alone, we find the case for association based upon poorly preserved skull fragments unacceptable, particularly when de Broin (1977: 151) claims that the cranial material from Leval is insufficient for determination. The lower jaw she refers (1977: pl. 8, figs 3–4) to *Palaeotrionyx vittatus* (Pomel) is in itself indeterminate: the fragment is associated with *Eurycephalochelys* and *T. levalensis* purely on size, which although convenient lacks justification. De Broin is correct in her assumption that a number of large trionychids were present in the Lower Eocene, with large skull and postcranial material recorded from both Europe and North America. It is likely, however, that the erection of a new subfamily may prove more acceptable than the reference of all known material to the 'comprehensive genus' *Palaeotrionyx*. A similar argument to that for *Eurycephalochelys* may also be put on behalf of *Conchochelys admirabilis* Hay (1905); from the original figures this bears little resemblance, except for size, to *Palaeotrionyx, sensu* de Broin.

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Fossil insects from the Lithographic Limestone of Montsech (late Jurassic–early Cretaceous), Lérida Province, Spain

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Synopsis

Fossil insects from the Lithographic Limestone (Upper Jurassic or Lower Cretaceous), Montsech, Lérida, Spain are described; their affinities and faunal significance are discussed. Seven orders of insects are represented (Ephemeroptera, Blattodea, Odonata, Hemiptera, Coleoptera, Diptera, Hymenoptera), three of which are previously unknown from this locality. The following six new species are described: *Mesopalingea lerida* gen. et sp. nov. (mayfly), *Artitocoblatta hispanica* (cockroach), *Condalia woottoni* gen. et sp. nov. (dragonfly), *Wonnacottella pulcherrima* gen. et sp. nov. (palaeontinid), *Chrysobotris* (?) *ballae* (buprestid beetle) and *Eobelus solutus* (eobelid weevil).

Introduction

The fossiliferous locality at Montsech has been known for many years; the first insects were described from the Lithographic Limestone by Meunier in 1902. Since then a number of collections have been made, the present paper being based on material collected by Dr H. W. Ball and Mr F. M. Wonnacott in 1955–60 and deposited in the British Museum (Natural History). The fossil insects are from a quarry in Lithographic Limestone 0·8 km south-west of Rubies (close to Santa Maria de Meyá) in the Sierra del Montsech, Lérida Province, north-east Spain (Figs 1–3). Some 50 m of strata are exposed and the succession has been described by Schairer & Janicke (1970).

The Lithographic Limestone is a facies development of the Caliza con Caraćeas Formation (Garrido-Megias & Rios Aragües 1972) and was deposited in a lagoonal–lacustrine environment which became stagnant at times (Schairer & Janicke 1970). The limestone has usually been considered to be Upper Jurassic in age, but work on the Ostracoda (Brenner, Goldmacher & Schroeder 1974) has now shown that the upper part at Rubies is late Berriasian to early Valanginian, i.e. early Cretaceous. The Ostracoda associated with the insect remains have been determined by Dr R. H. Bate as belonging to the freshwater genera *Darwinula* and *Cypridea*: one, *Cypridea wicheri* Wolburg ranges from the Upper Purbeck to Wealden (Bate, *in litt.*), indicating an early Cretaceous age for associated insect material (In.59464).

The insects occur in a fine-grained, well-cemented brown limestone. They are preserved as impressions, more or less compressed, and frequently show traces of cuticle. They were collected from scree material and their exact stratigraphical positions are unknown.

The biota is summarized by Condal (1951), Calatayud *et al.* 1953, Teixeira (1954) and Brenner *et al.* (1974). Apart from insects it comprises Foraminifera, Porifera, Crustacea, Ostracoda, molluscan ichnofossils, fish, amphibia, reptiles and plant remains, the latter including Charophytes.

Insect fauna

Although some of the specimens collected by Ball and Wonnacott have been briefly discussed (Wootton 1972) the collection has not previously been studied in detail. Some of the insects from Montsech mentioned by earlier workers, for example the ‘aculeate sphecid’ (Zeuner & Manning 1976: 155, Rasnitsyn 1980) have aroused controversy (Burnham 1978).

Bull. Br. Mus. nat. Hist. (Geol.) **38** (5): 381–412

Issued 31 January 1985

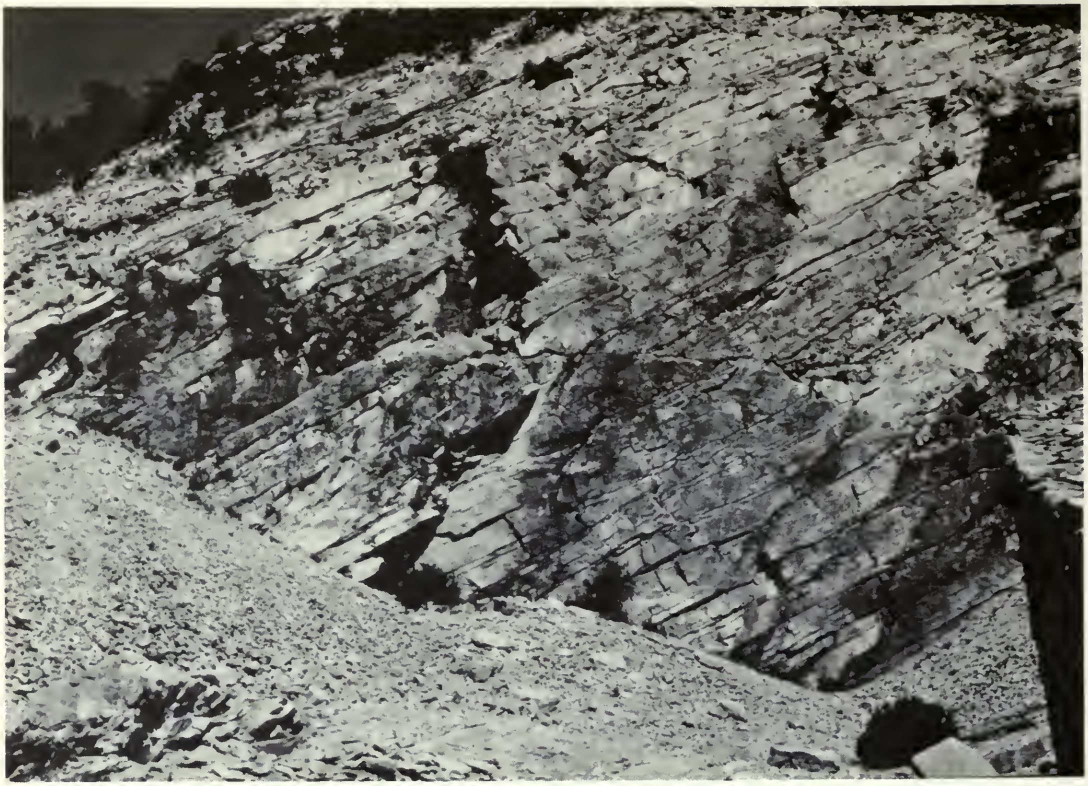

Fig. 1 Rubies Quarry, Lérida Province, Spain: general view. Photograph: H. W. Ball.

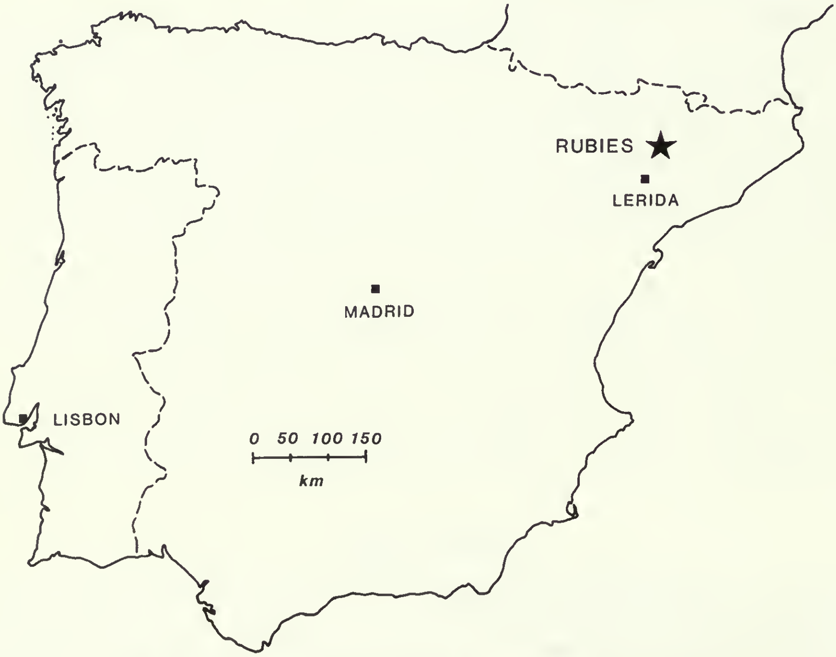
RUBIES
LERIDA
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Fig. 2 Location map showing position of Rubies site.

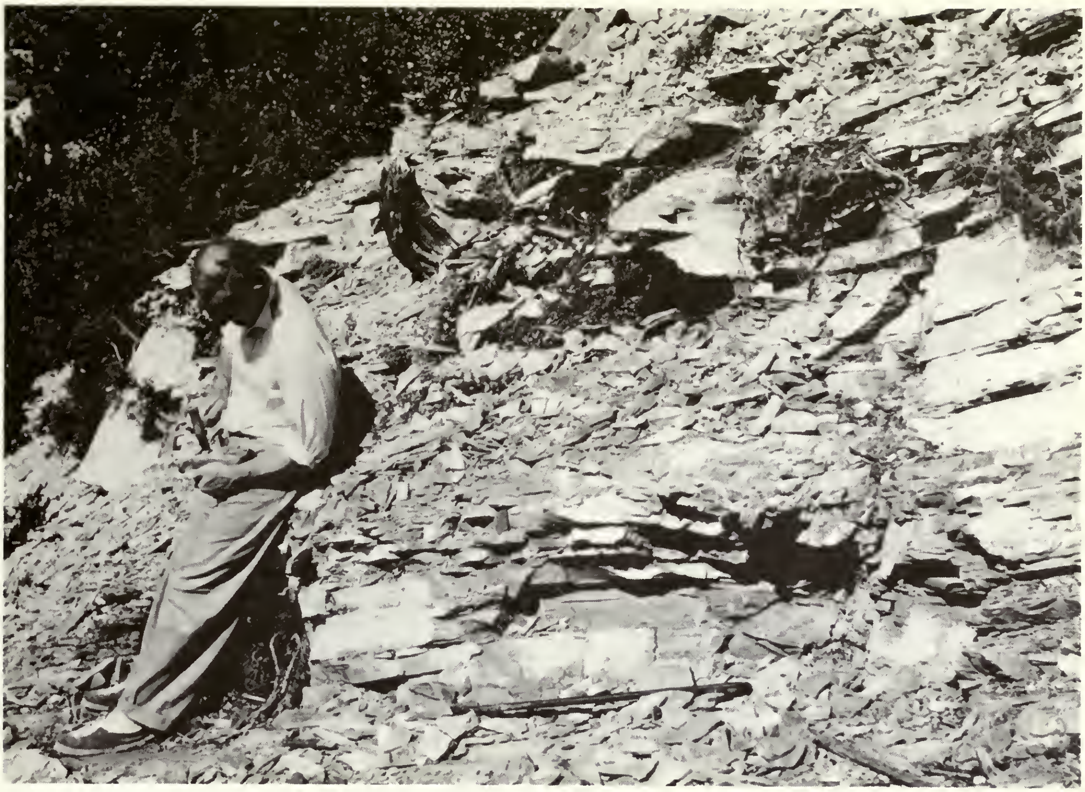


Fig. 3 Lithographic Limestone, Rubies Quarry, Lérida. Mr F. M. Wonnacott collecting. Photograph: H. W. Ball.

Wootton (unpublished Ph.D. thesis, 1961) discussed one species (Hemiptera, Palaeontinidae) at length and we have been fortunate in having access to his work.

Of the nine Orders of insects previously recorded from the Lithographic Limestone, two (Lepidoptera, Neuroptera *s.l.*) we consider to be based on incorrect determinations; the remainder are summarized below, with page numbers.

Ephemeroptera:	*Mesopalingea lerida* gen. et sp. nov.	384
Blattodea:	*Artitocoblatta colominasi* Meunier	387
	A. hispanica sp. nov.	388
Odonata:	*Condalia woottoni* gen. et sp. nov.	389
	Palaeaeschna vidali Meunier	391
Hemiptera:	*Wonnacottella pulcherrima* gen. et sp. nov.	392
	Pachypsyche vidali Meunier	391
	Acocephalites breddini Meunier	394
	Aleyrodoidea gen. indet.	394
	Geocorisae, gen. indet.	396
Coleoptera:	*Chrysobotris* (?) *ballae* sp. nov.	398
	Buprestidae gen. et sp. indet.	399
	Eobelus solutus sp. nov.	400
	Curculionidea, *incertae sedis*	400
Diptera:	Stratiomyidae gen. indet. (two species)	402
	Sciomyzidae gen. indet.	404
	uncertain affinities (two species)	404
Hymenoptera:	*Ephialtites jurassicus* Meunier	406
	Ichneumonidae gen. indet.	407
	Apocrita family indet.	408

The larva described as lepidopterous by Teixeira (1954: pl. 8, fig. 4) we consider probably dipterous but this is uncertain from the photograph. The dytiscid larva (Coleoptera) described by Condal (1951: 18) is an ephemeropteran nymph, while the sphecid (Hymenoptera, Aculeata) mentioned by Zeuner & Manning (1976: 155) we believe to be an ichneumonid wasp (p. 407). The various 'Neuroptera' mentioned by earlier workers are considered to be dipterous larvae (p. 403).

Systematic descriptions

Following the BM(NH) register number the letter (B) indicates the collection made by H. W. Ball & F. M. Wonnacott in 1960. The letter (W) indicates collections made by Wonnacott in other years.

Order **EPHEMEROPTERA**

Ephemeropteran adults have been recorded in Upper Carboniferous deposits (Chernova 1962), and from the Permian onward adult mayflies are found in many deposits (Wootton 1972); nymphal forms are less common in the fossil record. Kukalova (1968) described some Permian mayfly nymphs and Wootton (1972) mentioned the burrowing nymphs which are described below. Mayfly nymphs are the commonest insect fossils in the samples from Lérida, and although 19 nymphs were collected no adult mayfly was found.

Chernova (1977) described burrowing mayfly nymphs from the Siberian Jurassic in the families Palingeniidae and Bentiingiidae. McCafferty (1975) has described the burrowing nymphs of Recent species.

Superfamily **EPHEMEROIDEA**

Family **PALINGENIIDAE** Klapalek, 1909

This family is widespread in the Old World (Edmunds *et al.* 1976, McCafferty & Edmunds 1976), the nymphs being confined to fresh water. The nymphs described below are provisionally placed in this family, having similar mandibular structures which, in the Recent species, are important in the burrowing habit.

Genus ***MESOPALINGEA*** nov.

DIAGNOSIS. Palingeniid nymphs with broad flat mandibular tusks, toothed at the apex. Mandibles with two molar surfaces. Caudal filaments long, hairy.

NAME. *Meso* + *Palingea* (a Recent genus).

TYPE SPECIES. *Mesopalingea lerida* sp. nov.

Mesopalingea lerida sp. nov.

Figs 4, 6

1951 Dytiscid larva, Condal: 18; pl. 9, fig. 1.

DIAGNOSIS. As for genus.

NAME. Lérida Province, Spain.

DESCRIPTION. Nymph with broad, flat, mandibular tusks with inward pointing apical tooth on each tusk (Fig. 6). Outer margin of tusk with irregular edge formed by setal sockets (Fig. 6). Each tusk has large setal bases indicating that there were strong setae (not preserved). Long,

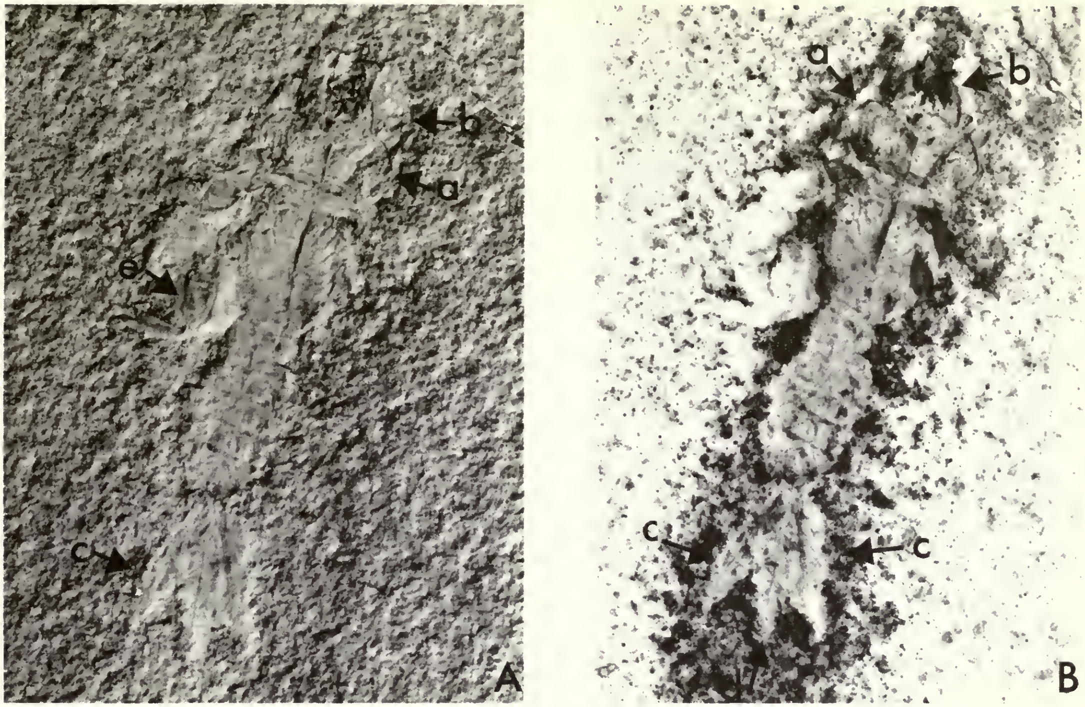


Fig. 4 *Mesopalingea lerida* gen. et sp. nov. (Ephemeroptera). Paratype. Nymph, In.49653, ×3. Photographed (A) dry, (B) wet. (a – compound eye; b – tusk; c – cerci; d – terminal filament; e – leg).

curved mandibles have double molar surface. Frons slightly produced in front of head. Smaller setal sockets are present along inner margin of the tusks. Antennae missing, antennal base visible in some specimens. Hypopharynx with lateral paraglossae present. Maxilla curved, pointed; lateral palp not preserved. Head broad with laterally protruding eyes, facets visible in some specimens. Eyes separated by a short distance in mid-line on top of head. Ocelli not visible. Prothorax short, mesothorax longer, metathorax with distinct wing pads with truncated apex. Forelegs with enlarged hairy tibia, rest of legs lost. Abdomen 10-segmented, trace of lateral gills, shape indeterminate: possibly some styli on abdominal segments. Cerci and terminal filament long, hairy (Fig. 4).

Holotype. In.59509 (W). Fig. 6.

Other material. In.44657 (W), In.49653 (W) (Fig. 4), In.49657 (W), In.59448 (B), In.59449 (B), In.59452 (B), In.59461 (B), In.59466 (B), In.59470 (B), In.59478 (B), In.59487 (B), In.59488 (B), In.59489 (B), In.59492 (B), In.59493 (B), In.59500 (B), In.59506 (W), In.59508 (W).

Dimensions. Nymph, length 15–22 mm (depending on instar).

Discussion. Mandibular tusks are characteristic of nymphs of several families of mayflies, where the tusks assisting in burrowing (Fig. 5). From the Jurassic palingenid *Mesopalingenia petersae* (Chernova 1977) the new species can be distinguished by the shape of the mandibular tusks, which are very broad in *lerida*. Even allowing for some compression in the tusks in the fossils, they are still wider than those of Recent species. Both *Mesopalingenia petersae* and *M. lerida* have an enlarged fore tibia.

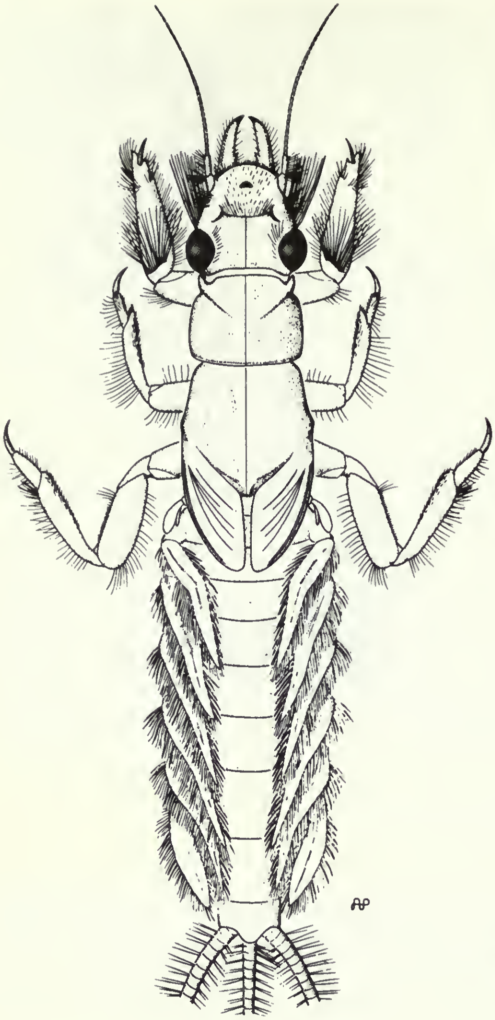


Fig. 5 Tusk-bearing Recent Ephemeroptera nymph, *Campsurus* sp., ×4. After Edmunds *et al.* 1976: fig. 432.

The fossil nymphs occur in two size groups but there is no difference in the morphology of the two groups other than size. They are therefore considered to be two instars of a single species. Condal (1951: pl. 9, fig. 1) figured the nymph of *M. lerida* but regarded it (p. 18) as a dytiscid larva (Coleoptera).

From the fossils we had to decide if they represented the actual insects or only the exuviae (cast skin) of the nymphs. When a nymph moults, the old skin splits along the back but none of the fossils showed any trace of this split. Today the delicate exuviae often wash together in backwaters where they may collect in some numbers, although they do not usually remain intact for long. The fossil nymphs were found sporadically in the limestone and did not occur together in lenses (H. W. Ball, personal communication). Also, though they lacked appendages, many of the bodies were intact. The indications are therefore that they were not the exuviae but the actual insects.

Recent mayflies are essentially fresh-water insects and there is no reason to believe the Jurassic species were any different. The burrowing habit is a specialized adaptation found in a number of families (McCafferty 1975, 1979) and it is interesting to find it in the Jurassic. But mayflies have a long history, perhaps dating back to the Upper Carboniferous (Crowson *et al.* 1967).

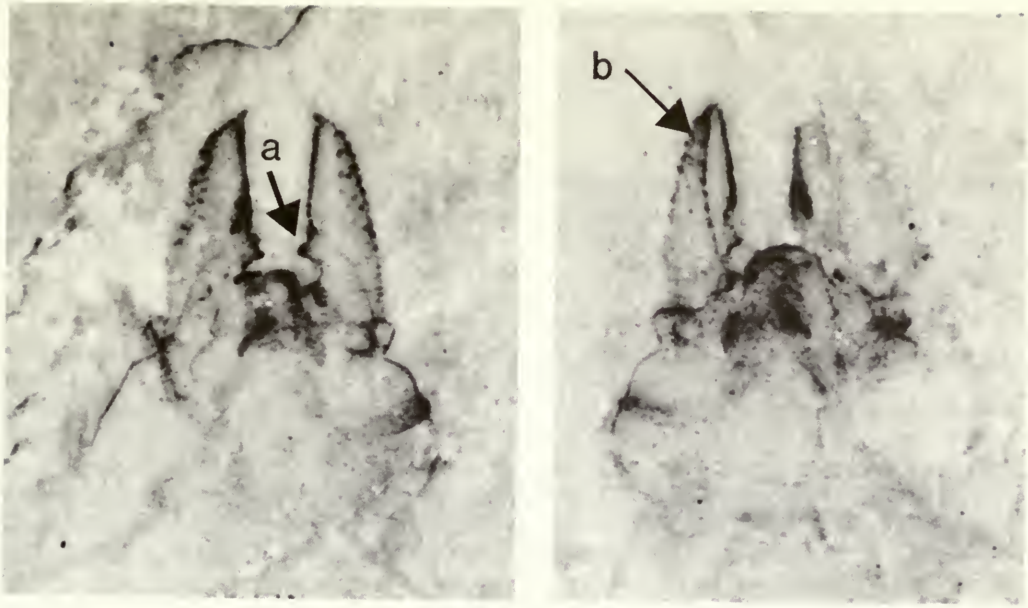


Fig. 6 *Mesopalingea lerida* gen. et sp. nov. (Ephemeroptera). **Holotype.** Head of nymph, In.59509, in part and counterpart, ×17. (a – mandible; b – tusk).

Order BLATTODEA

Cockroaches are common in the fossil record from the Upper Carboniferous onwards. Meunier (1914) described an almost complete cockroach, lacking only the hind wing, from the Lithographic Limestone of Montsech, which he named *Artitocoblatta colominasi*. Condal (1951: fig. 4) figured another specimen from this deposit which he identified as *A. colominasi*. From the photograph this specimen seems to lack a head: perhaps it was crushed under the prothorax and so not visible. Teixeira (1954), in listing the plants and animals recorded from the Lithographic Limestone, included *A. colominasi*. There are four new cockroach specimens in the present collection.

Family **MESOBLATTINIDAE** Handlirsch, 1908

Genus ***ARTITOCOBLATTA*** Handlirsch, 1906

Type species. *Artitocoblatta gossii* (Scudder 1886), by monotypy. Upper Jurassic, U.K.

Artitocoblatta colominasi Meunier, 1914

1914 *Artitocoblatta colominasi* Meunier: 4; pl. 1, figs 1a, 2a, 3a.
1951 ? Blattid, Condal: pl. 9, fig. 2.

Material. One incompletely preserved forewing. In.59465 (B), part and counterpart.

Dimensions. 6·5 mm long (incomplete).

Discussion. The costal and radial veins are missing but the entire anal and median areas are clearly visible. The complete forewing was about 7 mm long and compares well with Meunier's figures.

Artitocoblatta hispanica sp. nov.
Fig. 7

Diagnosis. Cockroach with short ovipositor in female.

Name. 'Spanish'.

Description. Head, prothorax and forewings missing. Costal vein of hind wing short, upturned. Radial veins strongly upturned. Median veins closely parallel towards margin. Anal area large, folded over in fossil. Ovipositor valves clear, short; lateral lamellae slender. Cerci hairy. Part of leg visible showing spiny tibia. [Male unknown].

Holotype. In.59505 (W), part and counterpart. The only specimen. Fig. 7.

Dimensions. Hind wing 6 mm. Abdomen 4·5 mm (excluding ovipositor). Cerci 2·5 mm.

Discussion. Meunier's type figure of *A. colominasi* shows a female with the broad abdomen and typical shape of a Recent cockroach. Condal's (1951) specimen is also a female (Mrs J. Marshall, personal communication). Both resemble the majority of Recent cockroaches in lacking any trace of ovipositor lobes. *A. hispanica* has ovipositor lobes and is separated on the basis of this character. This is a structure which is very rare in Recent species but often well-developed in Palaeozoic and Mesozoic forms, where it may be much longer than in *A. hispanica*. The venation of the forewing is important for generic classification in fossil cockroaches and as this is missing in the only specimen of *A. hispanica*, it is only tentatively placed in the genus *Artitocoblatta* Handlirsch. There it is associated with broadly similar species (with ovipositors) described by Vishnyakova (1968) from the Jurassic of Karatau. *A.*

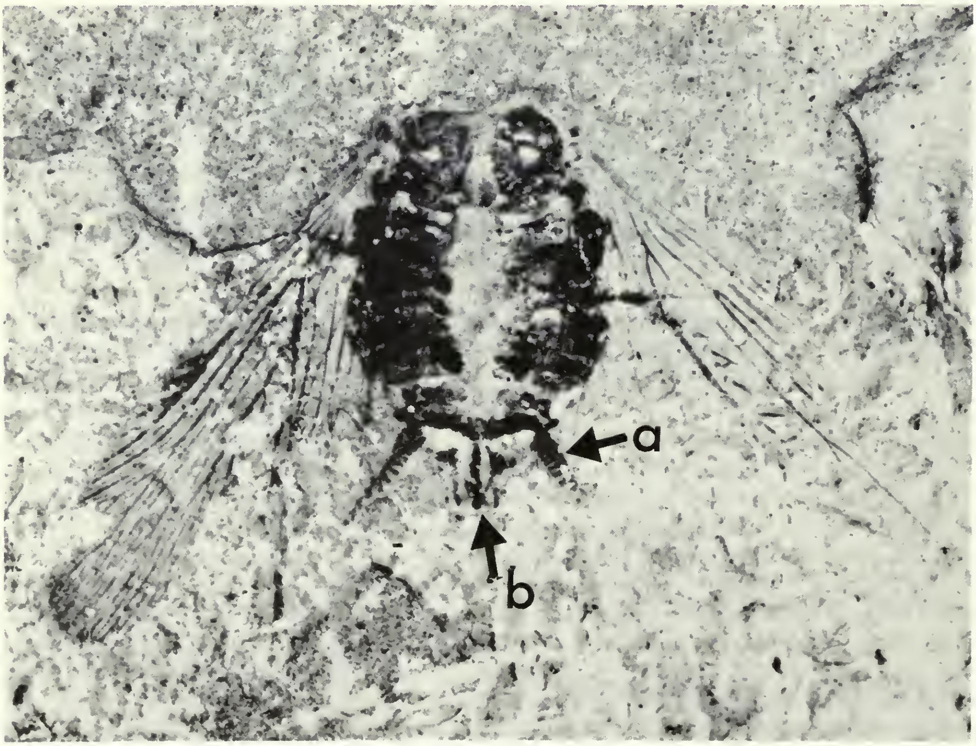


Fig. 7 *Artitocoblatta hispanica* sp. nov. (cockroach). **Holotype.** In.59505, ×13. (a – cercus; b – ovipositor).

hispanica can be distinguished from *A. asiatica* Vishnyakova by the shape and proportions of the ovipositor lobes and cerci.

Judged on the size of the hind wing, *A. hispanica* may well have been capable of flight like many Recent species of *Ectobius*.

Blattodea, *incertae sedis*

Specimen no. 1 is part of the forewing of a cockroach but is very incomplete and lacks the main diagnostic features for interpretation.

Material. In.59494 (B). 2·5 mm long (incomplete).

Specimen no. 2 also lacks the features used for generic interpretation but is part of the forewing showing typical intercalary veins of a cockroach.

Material. In.59459 (B). 3·5 mm long (incomplete).

Condal (1951: pl. 9, fig. 2) illustrates an almost complete cockroach which is not named. It is much larger (*c.* 10·8 mm long) than any currently known species from Lérida, but the original specimen has not been re-examined.

Order **ODONATA**

Suborder **ANISOPTERA**

The Lithographic Limestone of Lérida has yielded two species of dragonfly, both belonging to the extant suborder Anisoptera. One is an adult and the other is a nymph, but they are not related.

Family **LIBELLULIDAE** Latreille, 1802

Genus ***CONDALIA*** nov.

Diagnosis. Anisopteran with four antenodals in the forewing.

Name. For Dr L. Ferrer Condal.

Type species. *Condalia woottoni* sp. nov.

Condalia woottoni sp. nov.

Figs 8, 9

Diagnosis. As for genus.

Name. For Dr Robin J. Wootton.

Description. A single right forewing, well preserved except near apex where affected by a micro-fault. Venation as in Fig. 9. Nodus approximately two-thirds of wing length from base; only 4 antenodals (Ax), basal 2 stronger than distal 2. R_3, R_4 and distal parts of primary intercalary vein IR_3 and MA sinuous; secondary intercalaries Rspl and Mspl reduced; sectors of arculus not stalked; no crossveins in cubital, bridge, and median spaces.

Holotype. In.59491 (B). The only specimen. Fig. 8.

Dimensions. Preserved length of forewing 34 mm; maximum width 12·5 mm.

Discussion. Wootton (1972) briefly referred to this fossil and identified it as belonging to the Libelluloidea, an extant superfamily of Anisoptera which is considered advanced, and is

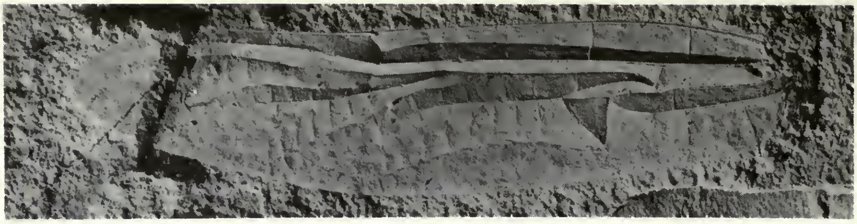


Fig. 8 *Condalia woottoni* gen. et sp. nov. (dragonfly). **Holotype.** Right forewing, In.59491. Counterpart, coated with ammonium chloride, ×2·75.

otherwise unknown before the late Caenozoic. Zherikhin (1978) doubted this identification and determined the photograph received from Wootton as that of a gomphid. Pritykina (1980) awaited confirmation of the systematic placing of this fossil.

The forewing of *Condalia* is undoubtedly that of an anisopteran dragonfly. The triangle, subtriangle and supratriangle resemble those of the extant genus *Aethriamanta* (Libellulidae, Urotheminae) (Fraser 1957: fig. 59.2) but are also similar to those of the living *Onychogomphus* (Gomphidae, Gomphinae) (Fraser 1957: fig. 48) and extinct *Necrogomphus* (Handlirsch 1906–08: pl. 47, fig. 8). The small number of antenodals in *Condalia* is not typical of Anisoptera. Gomphidae have many more antenodals, although reduction of these cross-veins does occur in the Libellulidae: in *Macrodiplax* (Urotheminae) there are six antenodals in the forewing and five in the hindwing (Fraser 1957: fig. 58). In *Nannophya* (Libellulidae, Brachydiplactinae) there are four antenodals in the hindwing and there may be as few as five antenodals in the forewing. The arculus in *Nannophya* is advanced in lying between the first and second antenodals (Fraser 1957: 118), which is also the situation in *Condalia*. A study of the BM(NH) collection has failed to reveal any libellulid with only four antenodals in the forewing. The nodus in *Condalia* is distant from the wing base, as in *Macrodiplax* and some other Anisoptera, but not Gomphidae. *Condalia* also resembles Urotheminae in that the sectors of the arculus diverge from their origin and the distal antenodal is complete: however, in *Condalia* the primary antenodals do not appear to be reduced as in Urotheminae (Fraser 1957: 106).

If the reduction of the antenodals is a specialization of the Libellulidae within the Anisoptera then Wootton's identification is correct. The extreme reduction of antenodals in *Condalia* becomes a unique specialization, while the triangle remains in a primitive state. Hennig (1981: 352) doubted the identification of modern families of the Anisoptera in the Upper Jurassic, and it is conceivable that *Condalia* represents a specialized genus from the

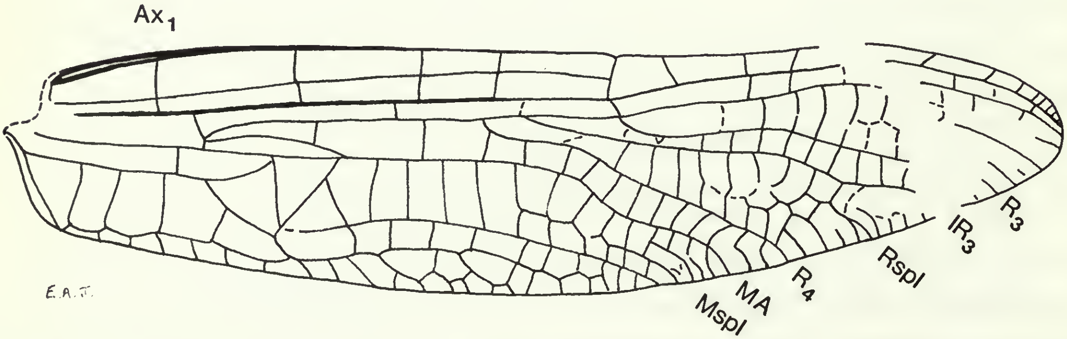


Fig. 9 *Condalia woottoni* gen. et sp. nov. (dragonfly). Right forewing, In.59491. Diagram of venation, ×4.

stem-group of the Anisoptera. However, until further work is done on the evolution of the Anisoptera in the Mesozoic, Wootton's identification cannot be rejected.

Anisoptera, Family uncertain

Palaeaeschna vidali Meunier, 1914

1914 *Palaeaeschna vidali* Meunier: 122–123, 125–126; pl. 2.
1951 *Palaeaeschna vidali* Meunier; Condal: 12–13; pl. 3, figs 3–4.

This nymph was described by Meunier (1914) as a new genus and species of the extant family Aeshnidae. The depository of the only known specimen was not given. Meunier's illustrations provide no evidence for placing *Palaeaeschna* in the Aeshnidae or any other anisopteran family. A similar conclusion has been reached independently by Prof. F. M. Carpenter for the forthcoming part **R** (3) of the *Treatise on Invertebrate Paleontology* (personal communication). However, the slender form of the nymph suggests that it is an aeshnoid rather than a libelluloid.

Examination of Meunier's published figure and photographs suggests that the former is inaccurate. The two lateral grooves on the abdomen, clearly visible in Meunier's enlarged photograph, suggest that the nymph is in ventral aspect. His interpretation of the eyes is doubtful, especially when the nymph is viewed in its correct orientation. He refers to wing buds in the text, but does not show them in his illustrations. In living dragonfly nymphs the rudimentary wings are located dorsally. The evidence for an anal pyramid and nine abdominal segments is not clear.

Condal (1951) described some further material which he considered belonged to this species, but did not resolve the systematic problems.

Mesozoic Odonata include a number of extinct families based on adults and assigned usually to the now relict suborder Anisozygoptera. A few Mesozoic nymphs have also been referred to this suborder, although the published work on *Palaeaeschna* does not suggest any affinity with Anisozygoptera.

Condal (1951) recorded a second dragonfly nymph identified by Oustalet and figured by Zeiller (1902); from the published information, the specimen should be considered with the dipterous larvae (species 2, p. 403).

Order **HEMIPTERA**

The plant bugs from the Lithographic Limestone of Lérida are known from few specimens, and no aquatic Hemiptera have been recognized. Five species are described, each based on a single example, only two of which are in the same family. Two species are based on wings alone; the others include body material. There is considerable size difference between the largest and smallest species. The fossils probably represent occasional strays from the neighbouring vegetation.

Calatayud *et al.* (1953: pl. 9, fig. 3) illustrate a possible hemipteran which Condal (1951: pl. 10, fig. 1) had previously considered an isopod. We have not seen the specimen and cannot comment on its affinities.

Suborder **HOMOPTERA**

Superfamily **CICADOIDEA**

Family **PALAEONTINIDAE** Handlirsch, 1906

The family is represented by two species in the Lithographic Limestone, one of which is described below; the other species, *Pachypsyche vidali* (Meunier 1902) has been studied by Wootton (1961, unpublished).

Genus *WONNACOTTELLA* nov.

Diagnosis. Palaeontinid differing from *Pachypsyche* Handlirsch, 1906, in possessing a narrower forewing and lacking venation between Rs and the anterior margin.

Name. For Mr F. M. Wonnacott.

Type species. *Wonnacottella pulcherrima* sp. nov.

Wonnacottella pulcherrima sp. nov.
Figs 10, 11

1971 Palaeontinidae, Wootton: fig. f.

Diagnosis. As for genus.

Name. 'Very beautiful'.

Description. The species is known from a single right forewing. The triangular wing has a small clavus which has nearly split off from the remigium along the claval furrow. The anterior margin is indented where the nodal line reaches the margin. Venation as in Fig. 11: R and Rs unbranched, curved posteriorly near the nodal line. M branched dichotomously, M_{1+2} separating distad of M_{3+4}. Cross-vein r-m short. R, Rs and M fused basally. CuA 2-branched; CuP single, very close to claval fold. Clavus with two unbranched anal veins. Nodal line traceable as a crease across R and Rs to stem M_{1+2} where it continues along the vein to its origin. The line, now stronger and vein-like, then crosses to CuA, follows the latter for a short distance and then continues independently to CuP, reaching CuP a short distance before the distal end of the clavus. The membrane is pitted distad of the nodal line and smooth basad of the line. The costal sclerite is present at the wing base, consisting of a raised area with about 10 transverse grooves more or less incised.

Holotype. In.59486 (W). The only specimen. Fig. 10.

Dimensions. Length 39 mm, width 16 mm.

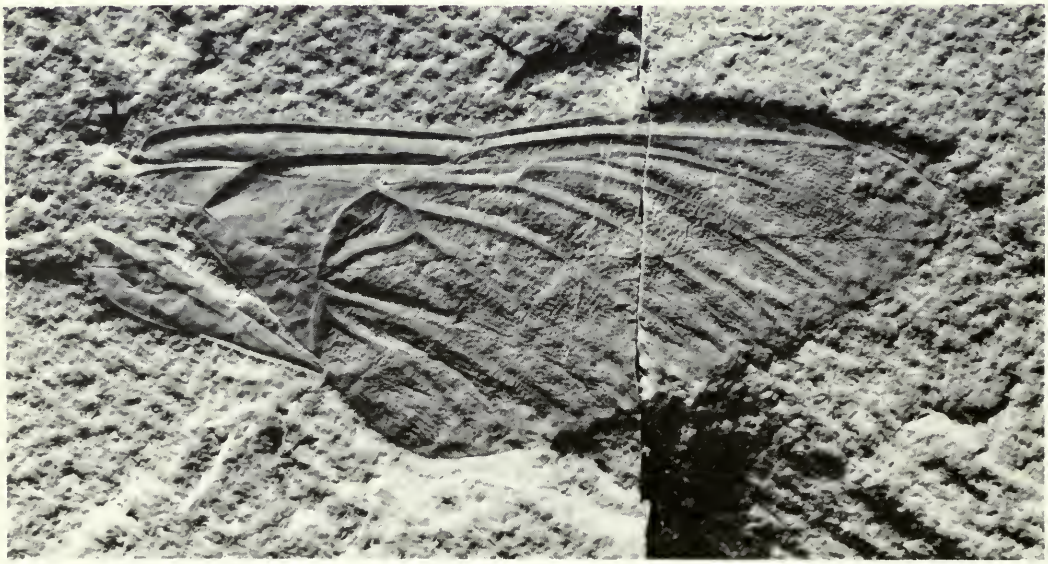


Fig. 10 *Wonnacottella pulcherrima* gen. et sp. nov. (palaeontinid). **Holotype.** Right forewing, In.59486, × 3. Arrow indicates costal sclerite.

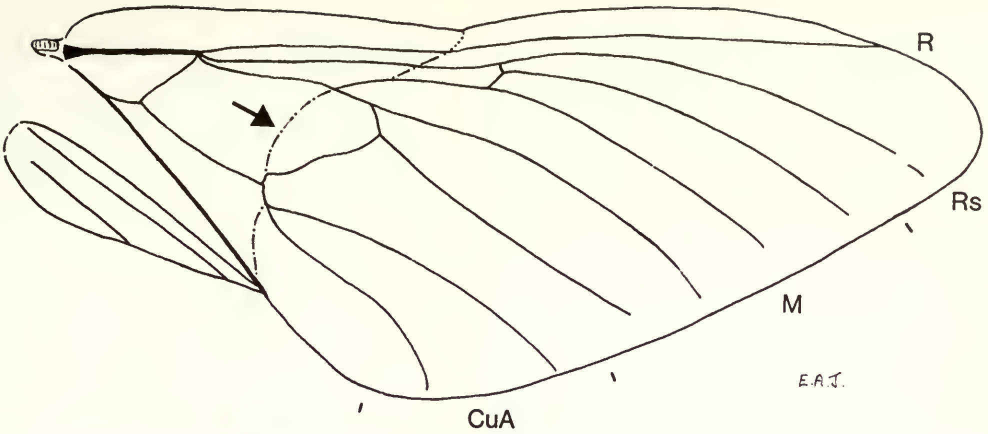


Fig. 11 *Wonnacottella pulcherrima* gen. et sp. nov. (palaeontinid). Right forewing, In.59486. Diagram of venation, ×3·3. Nodal line arrowed.

Discussion. The forewing of *Wonnacottella* is similar to that of *Pachypsyche* but is narrower, Sc and C are not free, m-cu leaves M_4 a little more basally, the nodal line follows M_{1+2} for part of its course and the clavus is apparently smaller.

Wootton (1961) suggested that the grooved area at the wing base of specimen In.59486 (now *Wonnacottella*) was a stridulatory file. He compared it with some extant cicadas where the grooved areas on the mesonotum are considered to be stridulatory files, producing sound when rubbed by the clavus. But examination of the file on *Chonosia crassipennis* Walker shows that in this species the anterior part of the costal sclerite at the wing base is also finely grooved: this sclerite is concerned with wing folding and not sound production (Myers 1928). The grooved area on the wing base of *Wonnacottella* is in the correct position for a costal sclerite; hence it was probably involved with flight and not in stridulation.

Bekker-Migdisova (1949) distinguished three groups of Palaeontinidae according to wing form. One of these, the Dipterygia, was characterized by narrow forewings with strengthened anterior margin which was considered a specialization for strong, rapid flight. *Wonnacottella* has a relatively narrow wing and the anterior margin is strengthened by the basal fusion of R, Rs and M; it can therefore be described as dipterygian (Wootton 1961). The wing shape of *Wonnacottella* resembles that of extant fast-flying moths of the family Sphingidae: the analogy is strengthened by the fact that the bodies of Palaeontinidae, where known, are broad like Sphingidae.

Wootton (1961) distinguished a group of late Jurassic–early Cretaceous Palaeontinidae comprising *Wonnacottella, Pachypsyche* and *Eocicada* (the last from the Solnhofen Limestone) which he considered to be 'clearly natural'. This group is characterized by the development of triangular forewings, with an extended anal angle, and R, Rs and M separting at a single point. This venational character is linked with narrowing of the forewing as discussed above, and narrow forewings appear to have arisen convergently in the Palaeontinidae (Wootton 1961). However, these particular modes of strengthening the anterior margin and the triangular wing form may well be unique specializations.

In Wootton's grouping only the genus *Eocicada* contains more than one included species, and from the illustrations it would appear that size difference is a useful interspecific character.

The nodal line in the forewing of extant cicadas separates the deformable and supporting zones of the wing in flight (Wootton 1981). Dimorphism of the membrane on either side of this line occurs in cicadas (Myers 1928) and is pronounced in *Wonnacottella*. Hinton (1948) suggested that the nodal line acts as a flexion line in the wing pads of the subterranean nymphs of extant cicadoids, enabling them to move backwards. The nodal line is developed also in Hemiptera without subterranean nymphs, but Hennig (1981) suggests that the form of the line in adult cicadas might be linked with the distinctive nymphal habits of these insects. Myers (1928) considered the nodal line in Palaeontinidae to be cicada-like, but further investigation of Recent and fossil forms is clearly necessary.

Hennig (1981: 273–4) considered that a marginal membrane and a marginal (ambient) vein were characteristic of cicadoids. This is certainly true of all extant cicadoids, although Hennig did not mention the Palaeontinidae. In *Wonnacottella* the wing margin is well preserved but a marginal vein and membrane cannot be seen. From the figures in Wootton (1971), these characters appear to be present in early Palaeontinidae; Wootton's accompanying discussion suggests a sister-group relationship between Palaeontinidae and Mesogereonidae, and a marginal vein is definitely present in the latter family. The loss (or migration to the margin) of this vein thus seems a specialization within Palaeontinidae.

Extant cicadoids are plant feeders and closely associated with woodland habitats.

Superfamily **CICADELLOIDEA**

Family **CICADELLIDAE** Latreille, 1825

Genus ***ACOCEPHALITES*** Meunier, 1904

Acocephalites breddini Meunier, 1904

[for synonymy list see Metcalf & Wade, 1966: 36]

Evans (1956) says that the single forewing (tegmen) upon which this species is based 'resembles those of recent cicadellids in all essential features'. We have not seen the specimen and follow Evans' classification. Meunier (1904: figs 1–2) published a line drawing, and no new illustrations have appeared subsequently. Meunier figured only a single anal vein, which is unusual in cicadellid forewings. From the size of the forewing (4 mm long) the insect had a wing span of about 10 mm.

Superfamily **ALEYRODOIDEA** (?)

? **Bernaeid,** ***incertae sedis***

Figs 12 (A–D), 13

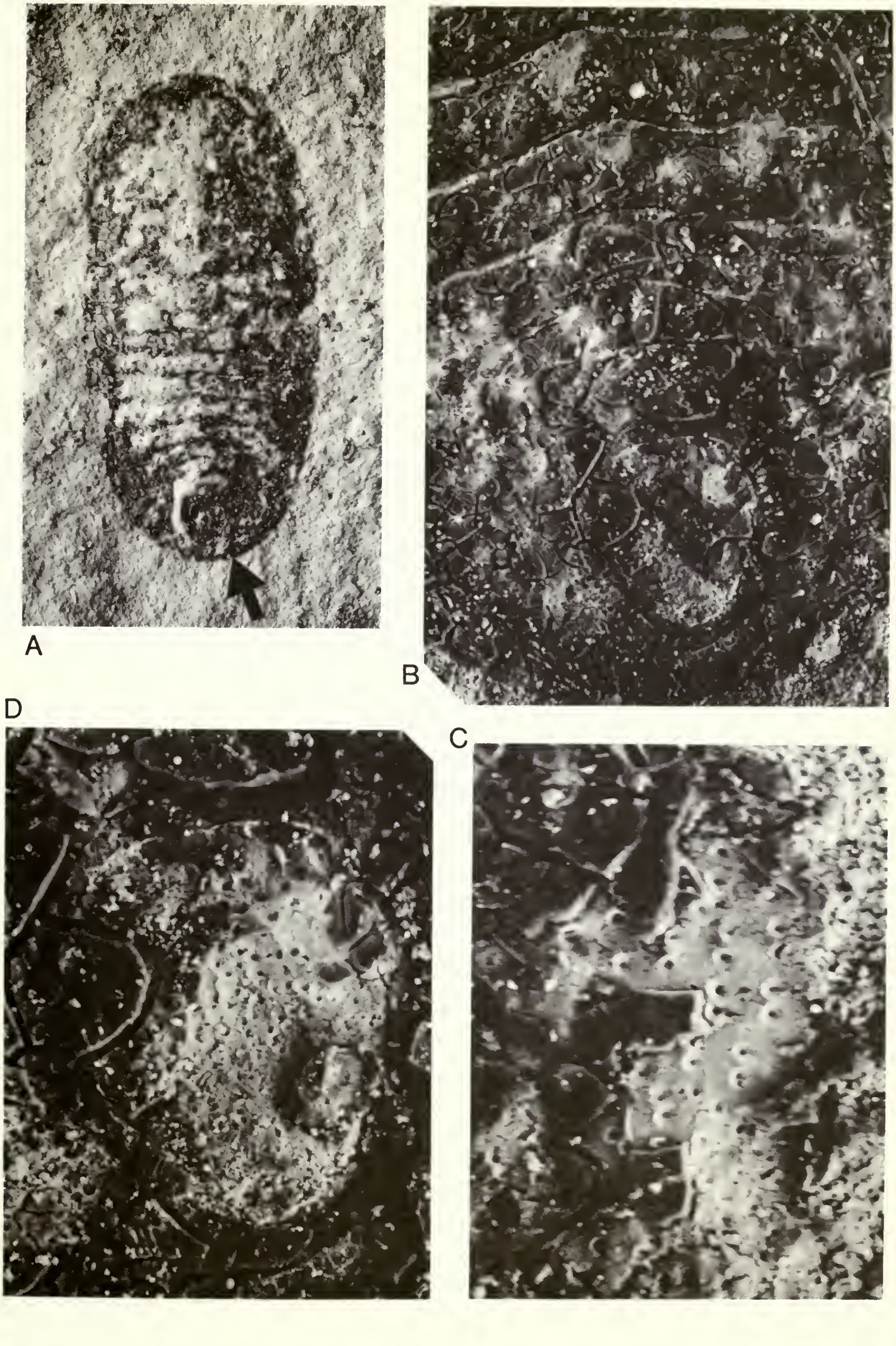
DESCRIPTION. Body elongate, rounded anteriorly and posteriorly, and slightly convex, with traces of a marginal rim (Figs 12A, 13). The segmental divisions do not appear to intersect the body margin. Dorsal surface and margin of ventral surface with micro-processes (1–2 μ) which in places show a rough alignment (Fig. 12C). Thorax with some weak transverse furrows and strong meso-metathoracic suture. Abdomen with well-developed segmentation, comprising seven broad and one narrow divisions. Anal area elongate and situated in a depression (Figs 12B, C). Whole body area including anus with traces of chitin.

DIMENSIONS. Maximum length 0·9 mm; width 0·4 mm.

MATERIAL. In.60600 (W).

DISCUSSION. The fossil resembles the dorsal disc of an aleyrodoid 'pupa' case in the shape and relative flatness of the body with its unbroken, rimmed margin, the form of the dorsal anal area, the fact that obvious segmentation is confined to the central area, and its small size. The possibility that it is the immature stage of some other superfamily of insects or belongs in another class of arthropods has been considered. However, from the available

Fig. 12 Aleyrodid (whitefly)? Dorsal disc of pupa case, In.60600. A, ×67 (arrow indicates anal area); B, hind end ×250; C, lateral margin ×675; D, anal area ×570.


A
B
D
C

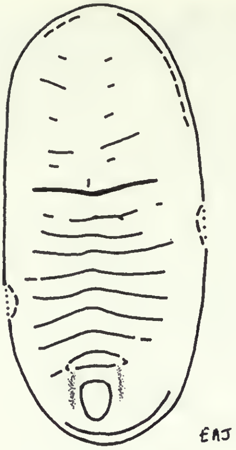


Fig. 13 Aleyrodid (whitefly)? Dorsal disc of pupa case, In.60600. Sketch, ×65.

information it most closely resembles an aleyrodoid. Amongst the Insecta it shows some resemblance to Coccoidea (scale insects) but the ultrastructure is unlike the pores found in the latter.

Hitherto, the earliest known whiteflies have been adults occurring in Lebanese amber (Neocomian–Aptian) (Schlee 1970). These do not belong to any extant family or subfamily but to the stem group of the Aleyrodoidea (Schlee 1970). Zherikhin (1980) referred these fossils to a new family Bernaeidae. Immature whiteflies have not been reported previously from the Mesozoic: in extant species they are usually found on the undersides of angiosperm leaves, although a few occur on ferns (Woodward, Evans & Eastop 1970: 425).

Suborder **HETEROPTERA**

Division **GEOCORISAE**

[= Gymnocerata Fieber, 1851]

Geocorisae, *incertae sedis*

Fig. 14

Description. A single body (female) preserved in partial relief; eyes clearly preserved on head; pronotum apparently parallel-sided and slightly concave anteriorly; scutellum prominent, triangular; basal parts of forewings preserved with traces of weak venation; claval fold visible on left forewing; legs preserved as weak impressions in the body; wings and body covered with fine microtrichia aligned with the longitudinal axis of body.

Dimensions. Body length 6·3 mm, width 2·1 mm.

Material. In.59495 (W).

Discussion. The general form of the body is typical of the Heteroptera (Geocorisae) but there is insufficient detail for family determination.

Order **COLEOPTERA**

Beetles are known in the fossil record from the Lower Permian. They are often abundant in deposits and are the commonest insect fossils in post-Permian times. Their strongly sclerotized structures, particularly the hardened elytra, are frequently fossilized.

Crowson (1975) summarized the evolutionary history of the Coleoptera with reference to the fossil record and comparative studies of extant species. Six beetles were found in the

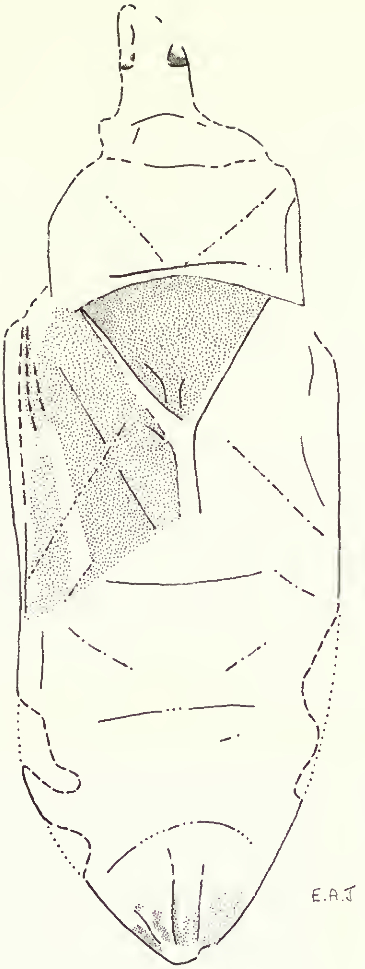


Fig. 14 Geocorisae bug. In.59495, ×20.

Lérida deposit, three of them (the weevils) being mentioned by Crowson (1975) but without any details. The remaining three specimens are placed in the Buprestoidea. One clearly shows features of the family Buprestidae, while the other two are provisionally placed here: only their outline shape suggests Buprestoidea.

The living Buprestidae or Jewel Beetles are essentially a tropical group and less common in the temperate regions. Although there are references to possible buprestid beetles in the Mesozoic (Crowson 1975) the species described below is the first positive record. The pattern, shape and especially the spined apex of the abdomen are typical of some genera of extant buprestids and indicate an early evolution of this group of beetles. If the larvae of the fossil buprestids had similar habits to extant ones, then they may well have bred in plants; many Recent species breed in gymnosperms.

The 'dytiscid larva' figured by Condal (1951: pl. 9, fig. 1) is a nymph of *Mesopalingea lerida* gen. et sp. nov. (Ephemeroptera); see p. 384.

Ponomarenko (1977) deals with Mesozoic beetles and, although no Buprestidae are included, gives a detailed account of the weevils found in the Jurassic of the U.S.S.R. These, together with the weevils described below, are the earliest known and show a remarkable similarity to extant species. This suggests a much earlier evolution of this specialized group, which was obviously well developed by the Jurassic.

Superfamily **BUPRESTOIDEA**

Family **BUPRESTIDAE** Stephens, 1829

Genus ***CHRYSOBOTRIS*** Eschscholtz, 1829
[= *Chrysobothris* auctt., incorrect subs. emend.]

Type species. *C. chrysostigma* (Linn.), by subsequent designation of Westwood, 1838.

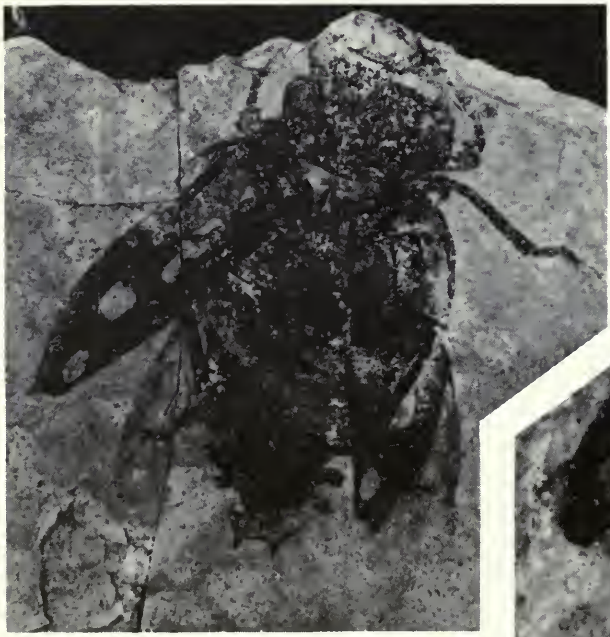
Diagnosis. Elytra truncate; anal sternite deeply incised; fore femora with broad tooth.

Chrysobotris (?) ***ballae*** sp. nov.
Fig. 15

Diagnosis. Buprestid with prominent pattern on elytra.

Name. For Mrs H. W. Ball, who collected the specimen.

Description. Pronotum large, broad, apparently unmarked. Elytra with paler symmetrical patches, probably four on each elytron. The pattern is made up of a smooth oval spot subapically, a fairly regular, slightly rectangular spot anterior to this and then an elongate patch. Finally at the base of the elytron there is a small patch which is only preserved on one elytron. Apex of elytra pointed, with short, concave terminal margin. Outer margin curved, elytra slightly broader in basal half. Hindwings only faintly visible, about the same length as the elytra. Foreleg with broad tooth on fore femora, mid-leg with four heavily spined tarsal segments, tibia narrow. Abdomen with strongly sclerotized tergites. Apical sternites deeply incised with two lateral points. Head obscured, antennae lost.



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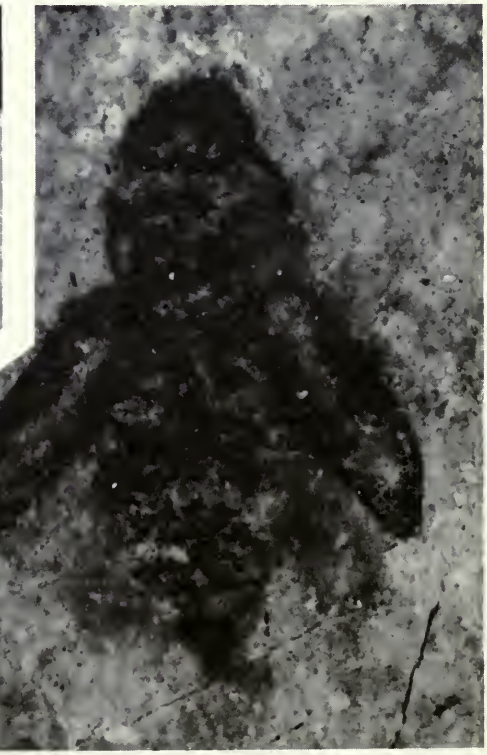

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Fig. 15 *Chrysobotris* (?) *ballae* sp. nov. (buprestid beetle). **Holotype.** In.59501, ×5.
Fig. 16 Buprestid beetle, species 1. In.59511, ×9.

Holotype. In.59501 (B). The only specimen. Fig. 15.

Dimensions. Length 15 mm, elytra 10 mm.

Discussion. Although this is a well preserved specimen, it has not been possible to see the typical Buprestid transverse suture on the metasternum. The general shape, however, especially the shape of the apex of the abdomen and well-sclerotized abdominal segments, is typical of most Recent Buprestidae. But many of the smaller detailed structural characters used in the generic classification of Recent Buprestidae unfortunately cannot be seen in the fossil, which can therefore only be provisionally placed in the genus *Chrysobotris*. This does not imply that we consider *Chrysobotris* to have been fully developed by the Upper Jurassic.

C. ballae is similar in pattern to a number of extant species of Buprestidae (Schaefer 1949) and bears a close resemblance to a number of species in *Melanophila* and *Phaenops*. The pattern on the elytra may be due to coloured patches, as in the similarly-patterned Recent species *Buprestis novemmaculata* Linn., or may be the result of structural differences in the elytra. These may have been in the form of depressions in the elytra of the living insect. The deeply incised abdominal sternite occurs in Recent species of *Chrysobotris, Melanophila* and *Phaenops*. The fossil differs from Recent species in the genus in not having serrations along the lateral margin of the elytral apices. The head and scutellum are not well preserved for positive identification as a species of *Chrysobotris*, but the left fore femur of the specimen has the broad tooth-like projection which is characteristic of Recent species of *Chrysobotris*.

The larvae of some species of Recent *Chrysobotris* feed in gymnosperms.

Buprestidae: species 1

Fig. 16

Although relatively well preserved in outline these two specimens, which we believe represent the same species, do not show sufficient detail to identify their relationship.

Description. Head broad, antennae missing. Thorax roughly square. Elytra with curved anterior margin, apex truncate, some striae and punctures visible on the elytra. Abdomen well sclerotized, apex narrower. Tarsi spiny. Hindwing well developed, indistinctly preserved.

Material: In.59604 (W); In.59511 (W).

Dimensions. Body length 9 mm; elytra 4 mm, width 1·5 mm.

Discussion. These specimens are tentatively placed in the Buprestidae. They have the general shape of Buprestoidea and Elateroidea but because of the well-sclerotized abdomen are placed in the former superfamily.

Superfamily **CURCULIONIDEA**

The weevils are a group of beetles with an elongate snout or rostrum in many species. They are specialized Coleoptera and 'can in many respects be regarded as the most highly evolved' (Imms *et al.* 1970: 811). They are almost exclusively plant-feeders, both in the adult and larval stages. Many species feed inside seeds while others are associated with various gymnosperms, including cycads. According to Arnoldi (1977), weevils were the most abundant and varied group of Coleoptera–Polyphaga in the Upper Jurassic of Asia.

There is no problem in identifying the fossils as weevils but the family placing is more difficult since many of the diagnostic characters are indistinct. Three specimens were collected; two are probably the same species while the third is distinct and certainly a different genus. The position of the insertion of the antennae on the rostrum is an important diagnostic character of weevils. In one specimen the antennae are inserted towards the tip of the rostrum but in another they are inserted nearer the head. The antennae cannot be seen in the third specimen.

The earliest known fossil weevils, from the Triassic of the U.S.S.R. (Arnoldi 1977), are very similar to the fossil family Eobelidae. Although the three specimens described below resemble some of Arnoldi's figures, none shows clearly either of the two most distinctive features of the family, namely the strongly margined prothorax and the very steep frons (the latter resulting from the emergence of the rostrum horizontally from the lower part of the head capsule). Specimen In.49648 appears to have the antennae inserted at the base of the rostrum, whereas in all known Eobelidae they are inserted at or beyond the middle of the rostrum. If the antennal insertion is really basal, then this species will not fit into any known weevil family.

Family **EOBELIDAE** Arnoldi, 1977

Although many diagnostic characters of this family are obscured in the fossil, the general shape indicates it belongs here and it is provisionally placed in the genus *Eobelus*.

Genus ***EOBELUS*** Arnoldi, 1977

Type species. *Eobelus longipes* Arnoldi, by original designation. Upper Jurassic, U.S.S.R.

Eobelus solutus sp. nov.

Fig. 17

Diagnosis. Eobelid-like weevil with long rostrum and well-sculptured elytra.

Name. 'Without impediment'.

Description. This is larger than the problematic species described below and the antennae are clearly inserted towards the apex of the rostrum. The antennae have at least nine segments and the rostrum, even allowing for some compression, is broad. Only the margin of the eye is visible. The elytra have a broadly truncate anterior margin and are pointed posteriorly. The surface of the elytra is covered with fine hairs arranged in rows, and inserted into prominent hair-bases. The tibiae are very hairy.

Holotype. In.59510 (W). The only specimen. Fig. 17.

Dimensions. Length 6·5 mm (excluding rostrum); rostrum 3·5 mm; femur 1·5 mm.

Curculionidea, ***incertae sedis***

Weevil: species 1

Figs 18, 19

Description. Few details are visible on either specimen. Antennae probably inserted towards the base of the rostrum, segments indistinct. Rostrum slightly curved. Coxae broad, long. Tibiae hairy. Three tarsal segments ending in a bifurcate claw. Body rounded.

Material. In.49648 (W) (Fig. 19); In.49658 (W) (Fig. 18).

Dimensions. In.49648: length 3·5 mm (excluding rostrum); rostrum 1·8 mm; hind femur 1 mm; hind tibia 1·2 mm. In.49658: body length 3 mm; rostrum 1·5 mm.

Order **DIPTERA**

While adult Diptera are known as fossils since the Triassic, their larvae are extremely rare in Mesozoic deposits. From the Cretaceous of Canada McAlpine (1970) described a possible Calypterate fly pupa while Brodie (1845) described the 'vermiform larva of a subaquatic

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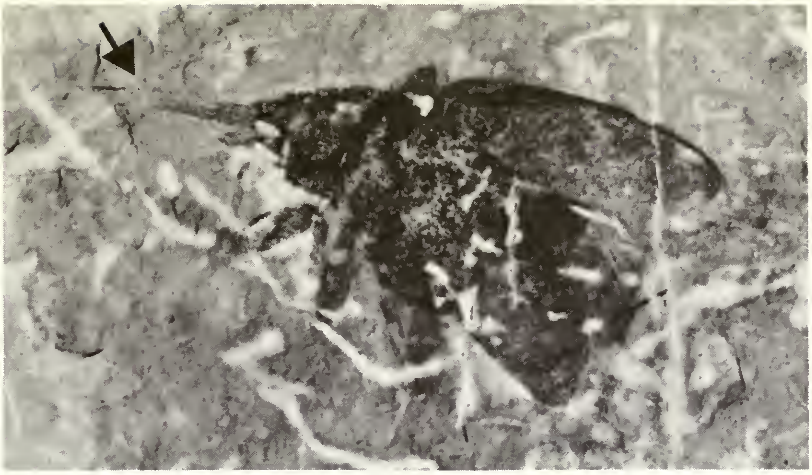

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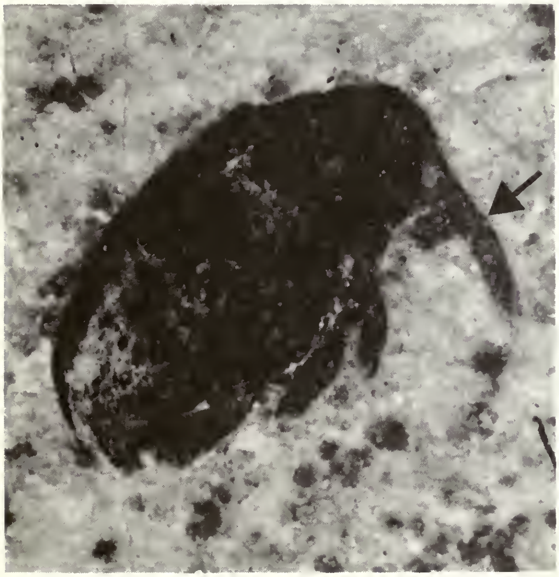

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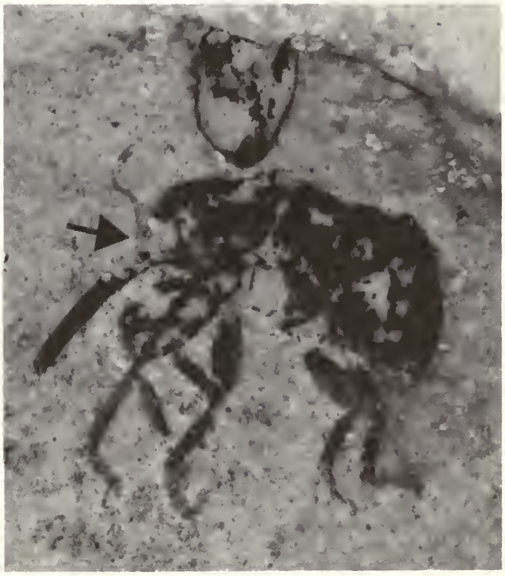


Fig. 17 *Eobelus solutus* sp. nov. (eobelid weevil). **Holotype.** In.59510, ×8. Arrow indicates insertion of antenna.

Figs 18–19 Weevil, species 1. Fig. 18, In.49658, ×21; arrow indicates rostrum. Fig. 19, In.49648, ×10; arrow indicates insertion of antenna.

dipterous insect' from the Upper Jurassic of Britain. There is an element of doubt over the identity of McAlpine's dipterous pupa while an examination of Brodie's type-specimen of 'vermiform larva' in the BM(NH) shows it to have a distinct head and sickle-shaped jaws; it is either coleopterous or neuropterous. Bode (1953) described a number of larvae and pupae from the Upper Liassic of Germany. The larvae he identified as nematoceran Diptera. He also described an adult fly, placing it in the Asilidae (Diptera, Brachycera). None of the larvae illustrated by Bode resembles the Spanish specimens, which are the earliest known Brachycera larvae.

Rohdendorf (1964) in his '*Historical Development of the Diptera*' dealt almost exclusively with the adult stages. Larvae of Recent Diptera are not easy to identify and much of their identification is based on a lateral view of the cephalopharyngeal skeleton. While there is no doubt of the dipterous nature of the Spanish specimens, further classification into families is difficult.

Larvae were described and illustrated from Lérida as early as 1902. Zeiller (1902: pl. 1, fig. 4) figured the larva of an insect which he considered to be Neuroptera (s.l.). We have examined the photograph and believe it to be a dipterous larva, showing the typical cephalopharyngeal skeleton, although we cannot place it in a family within the Diptera on the evidence available.

Condal (1951: pl. 5, figs 1, 3) figured insect larvae and quoted Oustalet as suggesting they were neuropterous (s.l.). The shape of the cephalopharyngeal skeleton shows clearly in Condal's pl. 5, fig. 1, which is similar to our species 2 (below). His pl. 5, fig. 3 shows a larva which Oustalet considered to be that of a dragonfly, but we think it is another typical dipterous larva, although less well preserved than most specimens in this formation.

Teixeira (1954) listed and figured the fossils from Lérida sent to him by Condal, but did not name them. The larva described as an 'aquatic coleopteran' (Teixeira 1954: pl. 8, fig. 5; not pl. 7, fig. 5 as in Teixeira's caption) is difficult to interpret from the photograph. Another larva is also illustrated in pl. 8, figs 4 (lower) and 4a: Teixeira considered it to be lepidopterous and compared it with the Sphingidae. He also compared the specimen with Condal's (1951: pl. 5, fig. 1) unnamed insect larva. We do not think these are lepidopterous: Condal's figure is clearly dipterous and we believe Teixeira's figure also represents a dipterous larva. From the size and shape we think it is similar to our stratiomyid species 2 below.

Eight positively identifiable dipterous larvae were collected at Montsech, and a further specimen may be dipterous but is poorly preserved. They represent several species which may well belong to unrelated genera. From the tentative identifications proposed below it appears that the larvae, if they had similar habits to Recent species, lived in a damp or fully aquatic, non-marine environment.

Suborder **BRACHYCERA**

Family **STRATIOMYIIDAE** Latreille, 1802

Dipterous larva: species 1

Fig. 20

Diagnosis. Dipterous larva with the skin covered with minute plates, typical of the family Stratiomyidae.

Description. The minute plates are about the same size as some found on Recent Stratiomyidae larvae (Rozkošny 1973), with which these fossils have been compared. On the last segment of the larva there is a slight thickening which may represent the posterior spiracle. The mandibular sclerites have a hooked tip and appear as paired slender rods.

Material. In.59503 (W) (Fig. 20, part and counterpart), In.59475 (B), In.59484 (B).

Dimensions. In.59503: length 14 mm, width 7 mm, mandibular sclerite 1·2 mm. In.59475: length 18 mm, width 6 mm. In.59484: length 16 mm, width 3·5 mm.

Discussion. The broad similarity to Recent Stratiomyidae, particularly in the form of the surface sculpturing, is striking. Fossil Stratiomyidae adults are known from the Eocene/Oligocene and are very similar to Recent species, even having similar colour pattern. Many Recent Stratiomyidae larvae are aquatic and have a circlet of hairs or two lobes on the posterior segment. The whole skin is rough or 'shagreened' and, in Recent species, the integument may be composed of hexagonal or oval plates which are of calcium carbonate. The function of this is not known but many species live in water rich in organic matter and thus with a low pH value. The calcium carbonate integument may well be an adaptation for survival in acid conditions which cannot be tolerated by other larvae not having this characteristic (McFadden 1967).

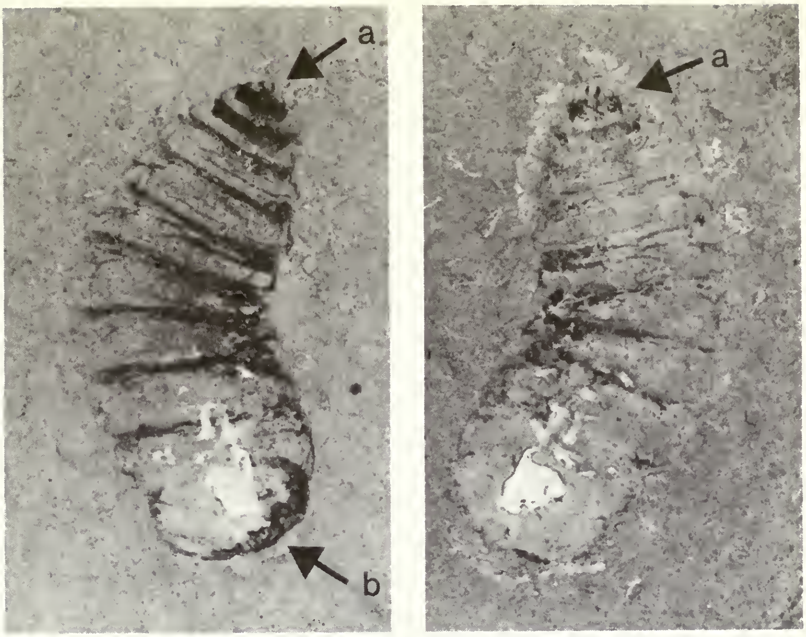


Fig. 20 Fly larva, Diptera species 1. In.59503, part and counterpart, ×4·5. (a – mandibular sclerite; b – posterior spiracle).

Specimen In.59475 has the integument covered with minute plates and is broadly similar to In.59503. Specimen In.59484 is indistinct with no trace of the sclerotized mouthparts, although an impression of the cephalopharyngeal skeleton is visible. There are two small marks at the posterior end of the larva which may represent a short process on the last abdominal segment. This specimen is only tentatively associated with the previous two.

Dipterous larva: species 2
Fig. 21

1902 Neurόptero (= Odonata); Zeiller: pl. 1, fig. 4.
1951 Neurόptero (= Odonata); Condal: pl. 5, fig. 1.
1954 Lepidoptera larva; Teixeira: pl. 8, fig. 4a.

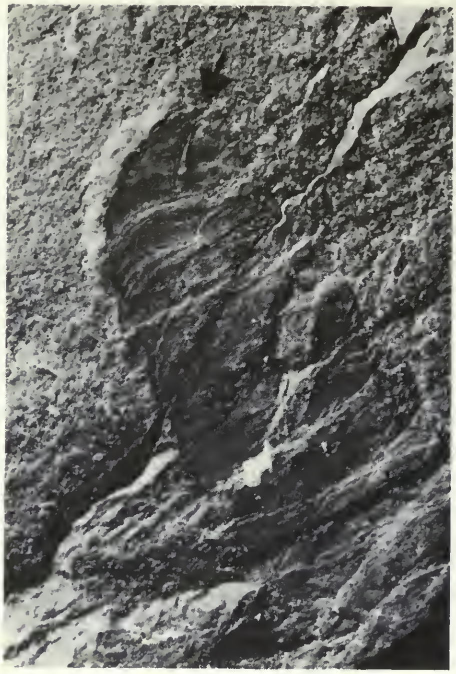
Diagnosis. Dipterous larva with minute plates on the body, similar to Recent Stratiomyidae.

Description. The skin is heavily folded but the cover of minute platelets, broadly similar to Recent Stratiomyidae, is visible. The mandibular sclerites are longer than those of species 1 and have a gently curved apex. The preservation of this larva is not as good as some of the previous specimens and only a little surface detail can be seen, but there is a thickening on the posterior margin of the last abdominal segment which suggests that the larva had two posterior spiracles.

Material. In.59469 (B), In.49650 (W) (Fig. 21).

Dimensions. In.59469: length 18 mm, width 5 mm, mandibular sclerite 3 mm (part and counterpart). In.49650: length 46 mm, width 13 mm, mandibular sclerite 6 mm.

Discussion. It is difficult to tell if In.59469, which is larger than species 1 (In.59503), is a later instar or a different species. In.49650 is particularly large while being broadly similar to In.59469; it is included with the latter as species 2. All have the roughened ('shagreened') skin like modern Stratiomyidae.



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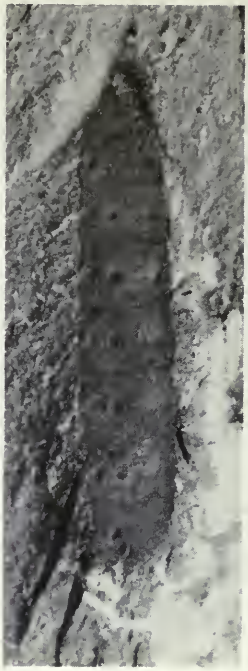

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Fig. 21 Fly larva, Diptera species 2. In.49650, ×1·5. Arrow indicates mandibular sclerite.
Fig. 22 Fly larva, Diptera species 3. In.49656, ×4.

Suborder **CYCLORRHAPHA**

Family **SCIOMYZIDAE,** *sensu* Hendel, 1902

Dipterous larva: species 3

Fig. 22

Diagnosis. Dipterous larva with lateral tubercles on abdominal segments.

Description. Although the cephalic part is missing the shape is unmistakably dipterous. Clearly visible are three rows of tubercles on each side of the seven preserved segments and traces of tubercles (or spiracular structure?) on the last segment.

Material. In.49656 (W).

Dimensions. Length 17 mm, width 5 mm (mandibular sclerite lost). Part and counterpart.

Discussion. This larva is very similar to those of Recent species of *Dictya* (Sciomyzidae), a group of snail-killing flies with aquatic larvae (K.G.V. Smith, personal communication); the lateral processes are quite distinctive.

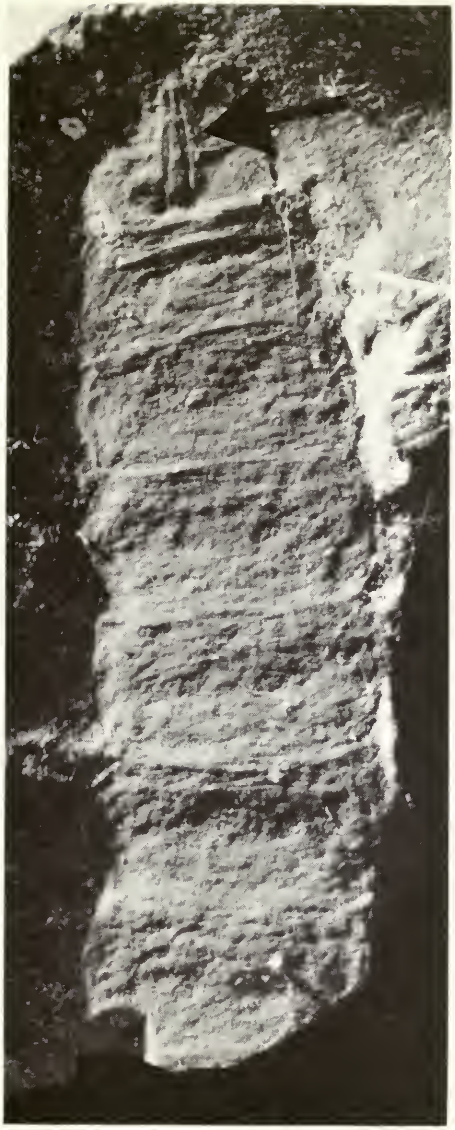
UNCERTAIN AFFINITIES

Dipterous larva: species 4

Fig. 23

Diagnosis. Dipterous larva with long, slender mandibular sclerites.

Description. The long, slender mandibular sclerites are curved at the apex and both are clearly preserved. The body is covered with minute granules (smaller than the Stratiomyidae



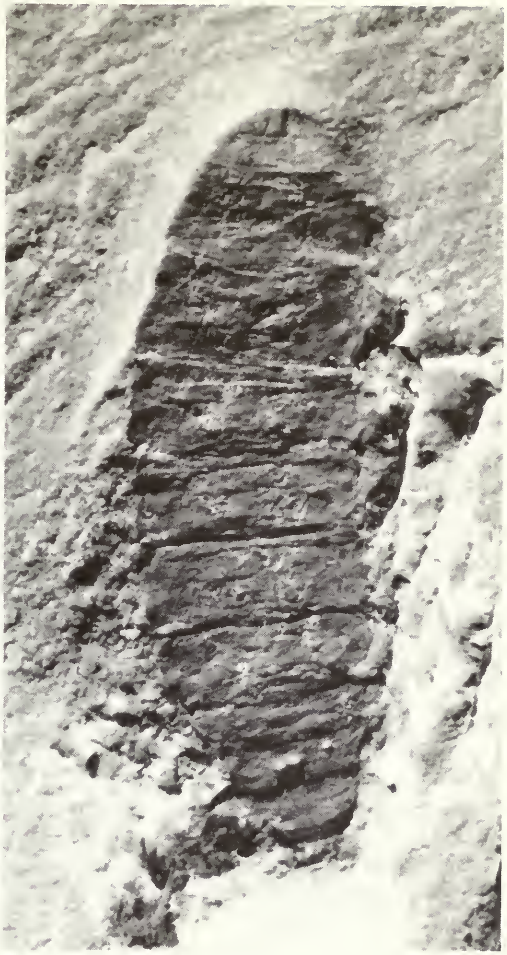


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Fig. 23 Fly larva, Diptera species 4. In.59455, ×5. Arrow indicates mandibular sclerites.
Fig. 24 Fly larva, Diptera species 5. In.59467, ×6.

platelets). On the fourth to eighth segments there are paired, round structures which are faintly preserved.

Material. In.59455 (B).

Dimensions. Length 23 mm (excluding projecting mandibular sclerite), width 7 mm, mandibular sclerite 4 mm.

Discussion. The lateral, round, paired, segmental structures along the body appear to be too close together, even allowing for compression, to be the two spiracles of a single segment; they may be short pseudopods. The general appearance of this larva is reminiscent of that of some Recent Ephydridae or the aquatic muscid *Limnophora*. Further possibilities are the larva of an aquatic member of the Dolichopodidae or Empididae. Although there is no sign on the specimens of the lateral or anal appendages even the possibility of it being the larva of one of the Athericidae should be considered (K. G. V. Smith, personal communication).

Dipterous larva: species 5
Fig. 24

DIAGNOSIS. Dipterous larva with minute surface granules.

DESCRIPTION. In this specimen the tip of the cephalopharyngeal skeleton is missing but at the base of it there is a short ridge at right angles to the sclerites which may be part of this cephalopharyngeal structure. On six of the body segments there are indistinct paired marks which could represent pseudopods. Further classification of this specimen is impracticable.

MATERIAL. In.59467 (B), part and counterpart.

DIMENSIONS. Length 17 mm, width 5 mm; mandibular sclerite lost.

Order **HYMENOPTERA**

Suborder **STEPHANOIDEA**

Family **EPHIALTITIDAE** Rohwer, 1920

Genus ***EPHIALTITES*** Meunier, 1903

TYPE SPECIES. *E. jurassicus* Meunier, by monotypy.

Ephialtites jurassicus Meunier, 1903
Fig. 25

1903 *Ephialtites jurassicus* Meunier: 4, 9; fig. 1.
1951 *Ephialtites jurasicus* Meunier (*sic*); Condal: 55; pl. 3, fig. 2.
1954 *Ephialtites jurassicus* Meunier; Teixeira: 141.
1975 *Ephialtites jurassicus* Meunier; Rasnitsyn: 43.
1981 *Ephialtites jurassicus* Meunier; Hennig: 402.

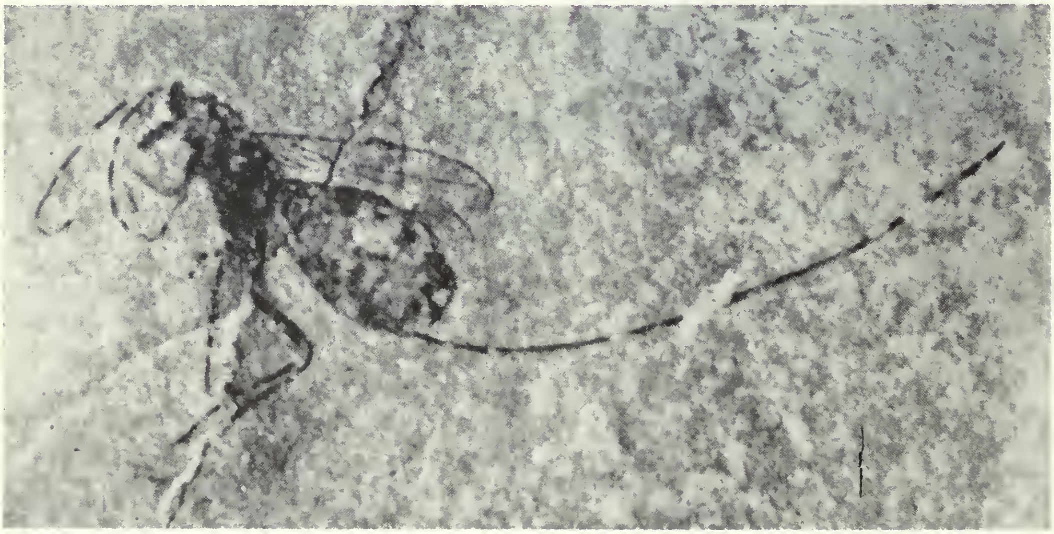

Fig. 25 *Ephialtites jurassicus* Meunier (parasitic wasp). Holotype, ×4. Specimen believed to be in Spain. After Meunier 1903: fig. 1.

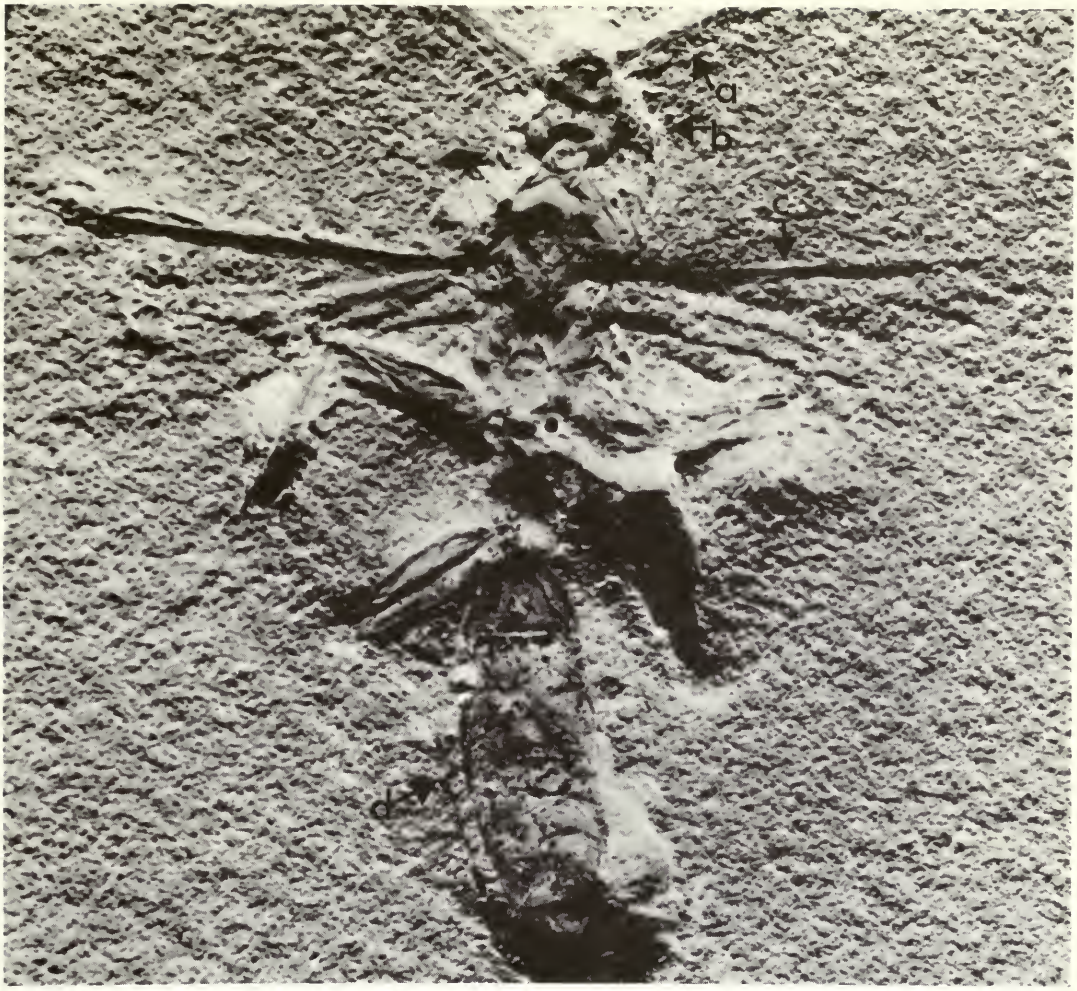

Fig. 26 Parasitic wasp, Ichneumonoidea. Part, ×6. Specimen apparently lost; photograph: R. J. Wootton. (a – antenna; b – head; c – forewing costal margin; d – abdomen).

The family Ephialtitidae was described in the Ichneumonidea but transferred by Rasnitsyn (1975) to the Stephanoidea. We have not examined the original material but from the published figure there is no reason to doubt Rasnitsyn's interpretation. *E. jurassicus* has a long ovipositor and is much smaller (7·5 mm) than the apocritan wasp described below.

Suborder **APOCRITA**

Superfamily **ICHNEUMONOIDEA**

Ichneumonoidea, *incertae sedis*
Fig. 26

In the introduction by Morris to the monograph on fossil bees by Zeuner & Manning (1976: 155), reference is made to a sphecid wasp fossil from the Jurassic of Lérida. This specimen had been considered by Manning as close to the ancestor of the bees. Burnham (1978: 119) commented on this, expressing some doubt about it. No other account of this specimen has appeared in print. The original specimen seen by Manning has not been re-examined but through the kindness of Dr R. J. Wootton we have been able to study a series of photographs of the part and counterpart.

It is now considered more likely that this specimen is an ichneumonid wasp (M. Fitton & M. Day, personal communication). Fig. 26 is reproduced from Dr Wootton's photograph. The costal margin of the wing looks thickened, the antennae are long and the abdomen expanded. The insect was large (20 mm body length), bigger than most other known fossil ichneumonids known, and has the general appearance of the Recent *Opheltes glaucopterus* Linn. (a sawfly parasite), although it is not necessarily related to this species. The possible host-group of ichneumonids, sawflies, were certainly present from the early Triassic and are common in the Jurassic rocks of Asia (Rasnitsyn 1969). Currently the earliest known ichneumonid wasps are from the Lower Cretaceous (Rasnitsyn 1980).

SUPERFAMILY INDET.

Apocrita, *incertae sedis*

Fig. 27

Specimen In.60602 (W) is clearly a hymenopteran and certainly in the suborder Apocrita. Few details can be seen, although structures are visible on the tip of the abdomen. One hind-leg, showing possibly an enlarged femur, is present. The base of the forewing has been preserved (Fig. 27) but unfortunately not enough of it to place this specimen in a superfamily with confidence. What is preserved is similar to some extant sphecoids (Riek *et al.* 1970: fig. 37.31–2). The specimen (10 mm long) is longer than *Ephialtites*, but only half the size of the ichneumonid discussed above.

Discussion

At least two-thirds of the fifty fossil insects found in the Lérida deposit are aquatic nymphs or larvae, or adult insects derived from aquatic larvae.

It is interesting that all the aquatic juvenile forms found are either bottom-dwellers (Ephemeroptera) or perhaps in a few cases dwellers in thick aquatic vegetation (Diptera); none are powerful swimmers like Recent water-boatmen (Hemiptera) or water beetles (Coleoptera). Mobile aquatic adult insects may be absent because they could swim strongly against the current that swept in the juvenile forms, none of which can be classed as strong

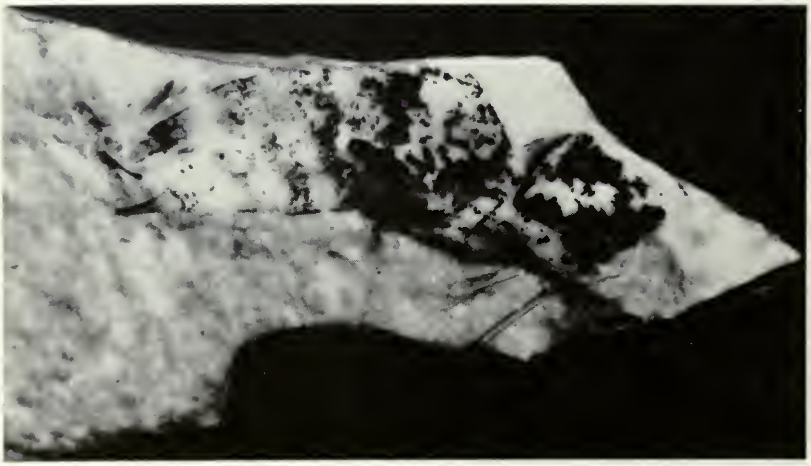

Fig. 27 Wasp, Apocrita superfam. indet. In.60602, ×7·5.

swimmers. This presupposes that the insects were transported by water. The mayfly nymphs, which form the largest single group, are almost certainly derived from a fresh-water environment with a soft bottom in which they would have burrowed. The fossil nymphs are slightly damaged, which suggests they did not live at the site of deposition but were transported there. The Diptera larvae would in general require shallow non-saline water high in organic content; i.e. stagnant conditions. Many modern stratiomyid (Diptera) larvae occur at the edges of lakes or slow streams where the vegetation is rotting freely and accumulating, and are less frequent in running water.

Cockroaches, bugs, beetles and wasps are all insects which would be associated mainly with terrestrial vegetation and not dependent on close association with water, but equally might be found in vegetation near water. There is no size sorting of the terrestrial species. For example, among the Hemiptera there is a large palaeontinid as well as a small aleyrodoid. So far no Orthoptera or Lepidoptera have been found in the deposit. Orthoptera, which are common in many Toarcian (Lower Jurassic) deposits, would be associated with open bush country and would not necessarily be found near water; neither would the Lepidoptera. The absence of adult mayflies is particularly interesting. Aquatic juveniles may have been carried away from their original habitat, or deposition may have been in the wrong season for adults to be present – although the presence of adults from other groups makes this less likely. The insect remains in the Lithographic Limestone are randomly distributed (H. W. Ball, personal communication). Many are relatively intact and consequently not likely to have been carried far from the areas in which they lived. The mayfly nymphs are common and possibly lived in muddy water-courses entering the lagoon. The presence of some sizeable insects suggests a warm climate.

Examination of the individual pieces of rock on which fossil insects were found shows that there is small-scale lamination in an otherwise fine-grained and homogeneous limestone with no evidence of bioturbation and only a little current activity (Fig. 28). The surface of the rock around the fossil insects shows no signs of surface structures, infills or other evidence which would point to an exposed surface at any stage. The insect fauna includes a high

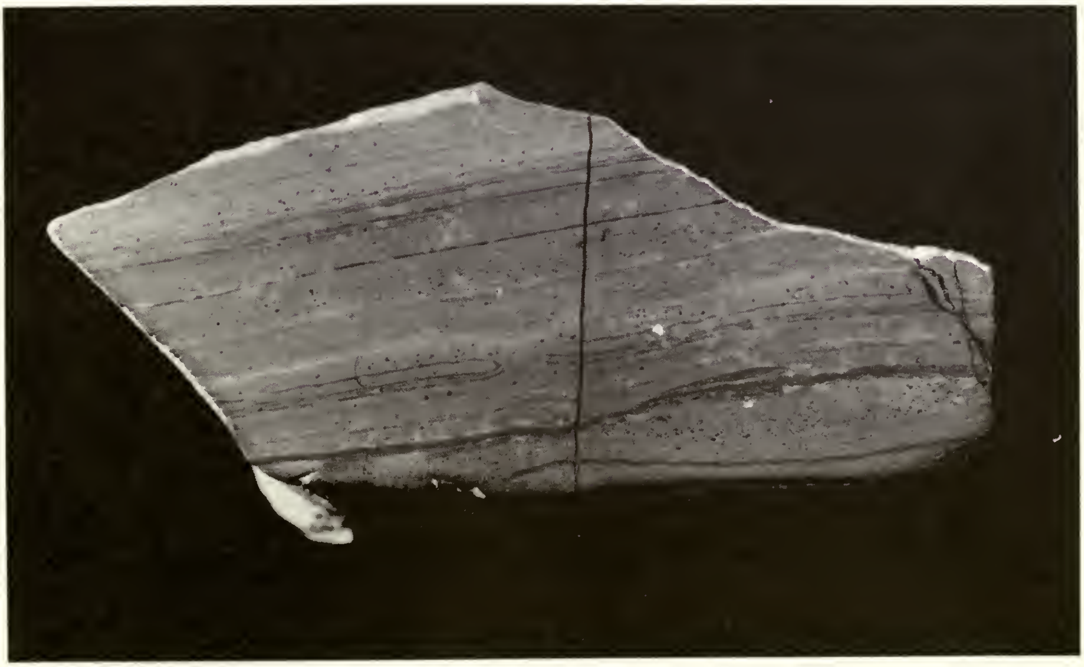

Fig. 28 Lithographic Limestone of Montsech: polished transverse section, ×2·5. (In.59497).

proportion of the soft-bodied forms. This suggests the specimens were deposited under very tranquil and anaerobic conditions. The fossils occur infrequently in the rocks, not apparently concentrated into lenses, although none were actually collected *in situ* (H. W. Ball, personal communication). Very little plant debris is associated with the insects and this suggests either that they were brought in separately or that some sorting (perhaps based on differential rates of settling of the organic debris) has occurred.

Evidence presented by Shairer & Janicke (1970) suggests fossilization in water, completely undisturbed on the muddy bottom of a lake or lagoon. In several of the specimens, the wings are spread out horizontally and these are species where the living insect would have normally folded its wings when at rest. Cockroaches, for example, normally keep the hind wing tightly folded below the forewings when at rest whereas the fossil cockroach (Fig. 7, p. 388) clearly has its hind wings outstretched, suggesting that its wings were open when it flew or was blown into the depositional environment. Schairer & Janicke (1970: pl. 21) illustrate what appear to be the drag-marks of a washed-in dipterous larva.

The insect fossils were deposited sporadically on very fine calcareous mud, and that this mud was laid down in cycles can be inferred from the laminations (Fig. 28). The periodicity of the laminations is unknown. The incorporation of organic detritus is visualized as a gentle 'rain' of water-logged material; the insects are unlikely to have been deposited as the result of storms or flash-floods. The fineness of the sediment suggests off-shore deposition, or that only fine material normally entered the basin of deposition. Such tranquil conditions are more likely in deeper water.

Acknowledgements

We are indebted to Dr H. W. Ball for advice on the manuscript, on the locality itself and for information on the specimens he collected. Dr C. R. Hill supplied us with palaeobotanical information and advice on the area. Mr D. L. F. Sealy gave us the benefit of his editorial experience. Dr R. J. Wootton gave us permission to use his photograph (Fig. 26) and to quote from his unpublished thesis (1961) on Mesozoic Hemiptera.

The following were very patient in answering our enquiries, often about very small fragments of insects: Dr P. C. Barnard, Dr J. Cox, Mr M. C. Day, Mr W. R. Dolling, Dr M. G. Fitton, Mr. D. Hollis, Dr B. Levey, Miss C. M. F. von Hayek, Dr W. J. Knight, Dr R. J. Lincoln, Mrs J. A. Marshall, Mr J. H. Martin, Dr L. A. Mound, Mr R. D. Pope, Mr K. G. V. Smith, Mr R. T. Thompson, Dr D. J. Williams, Dr A. R. Woolley; to all we offer our thanks.

The photographs, unless otherwise stated, were taken by the Staff Photographer, British Museum (Natural History), the stereoscans by Mr D. Claugher. Original line drawings by E. A. Jarzembowski.

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By the late W. F. Whittard, F.R.S. (Compiled by W. T. Dean)

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